DESCRIPTION OF THE SWIMMING BEHAVIOUR OF THE COMMON SMOOTHHOUND SHARK (*MUSTELUS MUSTELUS*) BASED ON TRI-AXIAL ACCELEROMETER DATA

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ABSTRACT

A thorough understanding of the behaviour and habitat use of sharks is critical for improving our understanding of the movement ecology of these threatened species. Direct observation of sharks is often difficult to accomplish in the marine environment where access to free-swimming individuals can be restricted by numerous factors. The miniaturisation and reduced costs of producing sensors for bio-logging has provided several solutions to overcome this obstacle. The accelerometer is a sensor that functions by recording changes in acceleration due to the dynamic motion of a body, and the static acceleration caused by gravity. Current accelerometer data-loggers can record at frequencies approaching 36 Hz, generating large datasets that are often stored to an internal memory for later retrieval.

In this study I demonstrate the potential for utilising tri-axial accelerometry as a method for characterising the movement of sharks. By attaching HOBO® Pendant G accelerometers to captive common smoothhound sharks (*Mustelus mustelus*), I was able to detect tail beat frequency, tail beat amplitude, and body posture. I then compared the accelerometer record to visual observations of the same sharks. A Wilcoxon signed rank test revealed no difference in tail beat frequency between the accelerometer data (0.76 ± 0.29 Hz; mean ± SD) and visual observation (0.77 ± 0.19 Hz; V = 61436.5, p = 0.3286). Steady swimming was readily identified (92.5 ± 6.4%; mean ± S.D.), but detection rates were much lower for resting (36.0 ± 45.0%) and fast start swimming (33.7 ± 32.4%), and especially gliding (4.7 ± 6.4%). Behavioural categorisation was achieved with the software package Ethographer by identifying the component frequencies and amplitudes of the accelerometer record with a continuous wavelet transformation and clustering the resulting spectrograph with a k-means clustering algorithm. This autonomous approach proved to be more than 100 times faster than manual annotation of the accelerometer record. Calculation of the body angle using the arcsine of acceleration in the surge axis resulted in similarly low detection rates of 22.8 ± 14.5%, 77.2 ± 11.0%, 47.6 ± 25.3% (mean ± S.D.) for inclined, neutral, and declined swimming respectively, when compared with visual observations.

Observational bias introduced by multiple observers may account for some of the discrepancy between the accelerometer and visual record for both the behavioural and postural categorisation. The clustering technique used for behavioural classification also has the potential to erroneously split behaviours that visually appear similar, but may be differentiated by varying tail beat frequencies or amplitudes. Furthermore, my behavioural definitions include transitional behaviours, such as the shift from swimming to gliding, which may not have clearly defined bounds.

True detection rates were calculated as the percentage of behavioural stats observed visually that were also detected in the accelerometer record. False detections were calculated as the percentage of behavioural states detected in the accelerometer record that were not observed visually. Despite low detection rates and high false detection rates for both behavioural and postural categorisation, the method still provides an objective, autonomous, and quick method for handling the large datasets generated by accelerometer data-loggers, warranting further research. Some value is noted in the ability of the technique to perform a coarse discrimination between periods of activity and inactivity, but the method does not yet provide reliable results for free swimming deployments. Recent applications of similar machine learning techniques where models are first trained are providing more accurate detection rates and together, with energetic analysis techniques like overall dynamic body acceleration represent the path forward for accelerometry.

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PLAGIARISM DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

ETHICS STATEMENT

The animal experimentation protocol for this research was reviewed and approved by the University of Cape Town Science Faculty Animal Ethics Committee. Research was carried out under Department of Agriculture, Forestry and Fisheries research permit number RES2012/22.

CHAPTER 1.
GENERAL INTRODUCTION, LITERATURE REVIEW, AIMS & KEY QUESTIONS

The relatively young field of quantitative movement analysis is currently facing a transformation characteristic of the progress of scientific development in many other mature scientific disciplines. Analysis techniques that were primarily descriptive and subjective are now supported by concepts and methodologies based on intensive statistical analysis. Traditionally, most young fields of study begin with observational descriptions of natural histories, before progressing on to more complex explanations and syntheses (Wold, 1956; Altmann & Altmann, 2003). The field of movement analysis is at this crossroads; as new technologies and statistical techniques are refined, a framework is being developed that enables researchers to begin outlining behavioural questions and testing hypotheses (Sims, 2012).

Movement ecology proposes a central paradigm for studying organismal movement by providing a conceptual framework integrating theoretical and empirical movement studies. The theory is based on the relationship between the four basic components of movement: internal states motivating an organism to move, the motion of the organism itself, orientation and navigation that drive where an organism moves, and the functions of individual and external factors affecting movement. With this approach, movement ecology enables a more unified and organised understanding of the causes, patterns, mechanisms, and consequences of organismal movement (Nathan et al., 2008).

Recent advances in tagging technology have facilitated the development of this approach. The ever increasing processing power of computers, miniaturisation of microprocessors, and the proliferation of global telecommunication networks is helping to create a multidisciplinary approach to monitoring the habitat utilisation, movement patterns and behaviour of marine organisms from the perspective of both organismal biologists and physical oceanographers (Block, 2005; Costa et al., 2010). This partnership is a direct result of the development of archival data-loggers incorporating sensors such as the animal-borne conductivity, temperature, and depth recorders (CTDs) that allow the recording of biological parameters from the animal and oceanographic parameters from the medium through which the animal is moving

(Hooker & Boyd, 2003). Sensors such as the CTD and others have the potential to shed new light on the various components of the movement ecology puzzle.

Early movement ecology studies focused on the change in position of the animal over time; answering the questions of 'where' and 'when.' Accelerometers have the capacity to reveal what occurs along these movement trajectories (Rutz & Hays, 2009). The fine-scale resolution of accelerometers allows for the detection of individual behaviours and also the energetic requirements that motivate larger scale movement; the 'how' and 'why' components (Nathan et al., 2012). Accelerometers offer many new opportunities for the study of behaviour, energetics, and the broader field of movement ecology, but also bring about a unique set of logistical challenges that will need to be overcome. Animal-attached accelerometers measure the dynamic acceleration of the body caused by movement, and the static acceleration caused by changes in the body angle of the animal with respect to the Earth's gravitational field. Accelerometers recording measurements at a sub-second sampling rate can accordingly measure the frequency and amplitude of each individual tail beat of a fish or shark. This high-resolution precision generates a large amount of data, excluding these devices from transmitting their complete data record and necessitating their recovery to download the large datasets from the internal memory of the data-logger (Whitney, Papastamatiou, & Gleiss, 2012).

The generation of large quantitative datasets is both an asset and limitation in the development of the accelerometry technique for the study of movement ecology. Sampling at frequencies necessary to get an accurate representation of tail stroke cycle can result in several million data points per deployment. There is then a need for the development of specialised techniques for the management, processing, and analysis of this new influx of information. Early progress has taken elements of time-series analysis and acoustic wave analysis like the Fast Fourier transformation, power spectral analysis, and wavelet analysis (Whitney et al., 2012). The software tool Ethographer utilises a continuous wavelet transformation to decompose the accelerometer record into its fundamental frequencies and amplitudes, and then passes this information to a k-means clustering algorithm that groups periods of similar behaviour based on their shared frequency and amplitude characteristics (Sakamoto et al., 2009). The ability of

these devices and associated analysis techniques was investigated on captive sharks using the common smoothhound shark (*Mustelus mustelus*) as a model species.

Studying Swimming Behaviour & Patterns

The course of scientific development within the discipline of ethology, as in other fields, most often begins with a fundamental description of characteristics before proceeding on to a more detailed explanation through the testing of hypotheses. In the case of animal behaviour, this description and explanation historically comes as a result of the direct observation of individuals in their natural environment (Wold, 1956). In fact, most ecological studies of animals in their natural habitat rely on visual observation; a direct reflection of the human tendency towards the primary sense of vision (Ropert-Coudert & Wilson, 2005). These observations provide the foundation for experimental observations and explanations that ultimately conclude in a synthesizing explanation of the original observational data (Wold, 1956).

In the field of marine biology however, the limited accessibility and poor optical quality of the underwater environment has restricted field observations of marine species (Ford, 1921; Strasburg, 1958; Cubero-Pardo, Herrón, & González-Pérez, 2011; Hammerschlag & Sulikowski, 2011). Dissolved matter and suspended particles absorb and scatter light, and depth and wave action limit the penetration of light into water and influence the visibility of submerged objects (Duntley, 1960). In the clearest marine ecosystems, underwater visibility reaches up to 30 m, but this is only a tiny percentage of the home range of a shark, for instance, which can occupy areas traversing thousands of metres (Nelson, 1977).

In addition to rare sightings of small animals distributed patchily at low abundances (Costa, 1993) across the vast scale of the three-dimensional underwater environment, other impediments to observation of marine organisms include their speed and agility (Block et al., 2002), and shy disposition with regards to divers (Nelson, 1977). The observation of sharks in particular is constrained by their tendency to spend much of the daylight hours at depths beyond the limit of SCUBA and by the fact that they are often nocturnal. While the advent of SCUBA has been invaluable for studying demersal marine organisms, including some species of sharks (McLaughlin & O'Gower, 1971), it seldom provides the necessary range and speed for observations of larger pelagic

species. Also hindering the study of sharks in the natural environment is the prospect of an occasional agonistic defensive display that can sometimes result in forceful contact to rapidly approaching divers (Johnson & Nelson, 1973; Martin, 2007). In studies of shark behaviour, there has also been considerable success in the use of bait to attract and aggregate sharks (Laroche et al., 2007). This methodology provides an excellent means to overcome many of the aforementioned obstacles to observation but does not reflect their natural behaviour (Nelson, 1977). Despite any behavioural impact, however, there is still value in describing the responses of an individual when presented with a food source (Hobson, 1963; Strong et al., 1992). Other tools currently being used to observe marine animals include photography, Underwater Visual Census (UVC), Baited Remote Underwater Videos (BRUV), and Remote Operated Vehicles (ROV; Boyd, Kato, & Ropert-Coudert, 2004; Stoner et al., 2008; Lowry et al., 2012).

Laboratory experiments of captive marine organisms offer a reliable method for making long term observations of individuals that are difficult to observe in the wild (Smale et al., 2004). Captive study provides experimental conditions not available in the field, such as increases in the precision of observations and the ability to control variables (Costa & Sinervo, 2004). Initial attempts at housing larger species of sharks in artificial enclosures proved unsuccessful as specimens often refused to feed, becoming emaciated and eventually dying of starvation (Essapian, 1962). Aquarists struggled to even transport some species to the aquarium following capture. Reliable methods for moving the scalloped hammerhead (*Sphyrna lewini*) eluded researchers until the last decade when successful intercontinental transportations were achieved (Arai, 1997; Young et al., 2002). Despite these accomplishments, some sharks still showed signs of stress such as discolouration and blemishes on the skin as a result of manual handling that lasted for months after delivery, some even requiring antibiotic treatment (Young et al., 2002). There is a popular notion that sharks are robust and hardy species, but even slight handling can induce a stress response (Rasmussen & Rasmussen, 1967). A recent review of shark husbandry in public aquariums (Koob, 2004), underscored best by the accomplishments in several aquariums at keeping large species like the whale shark (*Rhincodon typus*; Uchida, Toda, & Kamel, 1990), would lead one to believe that maintaining sharks in captivity is now a successful endeavour, yet species such as the white shark (*Carcharodon carcharias*) and manta rays (*Manta birostris* and *M.*

hamiltoni) remain difficult to support (Murru, 1990); a direct result of our limited understanding of these creatures.

Studies of animal behaviour assume that the actions being observed are representative of the animal's behaviour. This is true both in the field and in the laboratory where the presence of an observer may impact the behaviour of the animal being studied, or where observations may be misinterpreted due to the intrinsic bias of an observer (Rosenthal, 1966). Several examples of this have been recorded; Ollason and Dunnet (1980) described their observations of the breeding failures of the northern fulmar (*Fulmarus glacialis*) in the presence of observers. In her famous study of chimpanzees (*Pan troglodytes*), Jane Goodall initially faced considerable difficulty in approaching her subjects close enough for observation; prompting them to disappear into the dense forest. Gradual habituation to her presence over a period of months eventually allowed her the proximity she needed to observe the animals, but the original impact on their behaviour cannot go unmentioned (Goodall 1968). Other pitfalls to behavioural studies exist as a result of the presence of observers. An insufficient familiarity with the study species can lead to incomplete ethograms and the misinterpretation or overlooking of behaviours (Caine, 1990; Magnan, 1991).

Biotelemetry, the measurement of biological phenomena from a distance, and the related field of bio-logging, provide methods to observe behaviour and other characteristics of marine life without the constraints introduced by the environment or the observer (Wolcott, 1995; Boyd, Kato, & Ropert-Coudert, 2004). This transition from the perspective of the observer to that of the study species is what effectively removes the potential for the observer to affect the behaviour of the observed animal, and also eliminates the barriers to direct observation caused via the environment by facilitating remote measurements of free-ranging animals (Wolcott, 1995; Ropert-Coudert & Wilson, 2005).

While it is never the intent of a scientist to alter the natural behaviour of the species they are observing, there can still be limitations to the use of bio-loggers in the field. Attaching external devices to animals can impact their foraging behaviour and reproductive energetics (Wilson, Grant, & Duffy, 1986; Wolcott, 1995, Boyd, Kato, & Ropert-Coudert, 2004). Instruments can change the appearance of an individual,

causing them to appear larger and more dominant, or unattractive and less fit. For these reasons, logger packages were heuristically limited to 2% of the animal's body weight, although packages approaching 12% have shown no negative effects to swimming performance (Winter, 1983; Brown et al., 1999). More recently, logger induced drag has shown to be the primary factor impacting the streamlined swimming of some instrumented animals (Ropert-Coudert et al., 2007). Early research revealed loggers that increased cross-sectional area by 6.8% have shown negative impacts in the foraging success of penguins (Wilson et al., 1986). More recently, however, it has been shown that even loggers that do not increase cross-sectional area of the animal can increase body drag of swimming birds and that care should be taken to improve miniaturisation, streamlining, and attachment (Bannasch, Wilson, & Culik, 1994). In the specific case of sharks, dorsal fin attachment has proven a common method for tag placement (Hammerschlag, Gallagher, & Lazarre, 2011). Deployment duration and tag attachment method must be carefully designed to minimise the development of fin deformities (Jewell et al., 2011). Despite the ethical concerns of attaching devices to animals, bio-logging remains a much less invasive substitute than the lethal-sampling employed prior to the 1980s (Boyd, Kato, & Ropert-Coudert, 2004; Hammerschlag & Sulikowski, 2011).

BIOTELEMETRY AND BIO-LOGGING

Telemetered observations of sharks and other marine species provide a reliable means for overcoming the complications of direct observation, including the subject's general caution towards divers, their large home ranges, and the camouflaging nature of the underwater environment (Nelson, 1978). Devices initially consisted of simple ultrasonic beacons that allowed an animal's position and movement to be tracked (Trefethen & Dudley, 1957). However as advances in consumer technology resulted in the miniaturisation of electronic components, ever smaller and more complex devices were developed incorporating multiple sensors and channels (Standora et al., 1972; Wolcott, 1995).

The analysis of movement has been an important and key interest in the study of animals in their natural environments for quite some time (Holyoak et al., 2008), providing fundamental spatial and temporal information to help understand how a species utilises the environment. In some cases, indirect inferences of behaviour,

ecology, and social interactions can be made from this telemetry data. Ultimately however, with standard acoustic and satellite tags we are limited to just the animal's position in space and time; any behavioural conclusions are inferred (Rutz & Hays, 2009).

As an indication of the popularity and utility of spatial data, Tagging of Pacific Predators (TOPP) has successfully deployed over 4000 archival and satellite tags in their long-term study of large marine predators (Costa et al., 2010). Another global tagging and tracking initiative also born from the Census of Marine Life, the Oceanic Tracking Network (OTN), aims to create an international network of telemetry receivers to monitor the movements of tagged marine species (O'Dor et al., 2010). These movements represent a key component of an animal's life, helping to influence fitness, population structure and dynamics, and ultimately the evolution of a species. Further understanding of animal movements will enable enhanced management of the species, and of the environment (Nathan et al., 2008). In order to develop this understanding we must unearth what occurs along each movement trajectory. What are the individual's physiology, behaviour, foraging strategy, and habitat usage? How is climate change impacting fitness? More and more, researchers want to know the 'what' and the 'why' of these movements, and technological advances in the field of telemetry allow for some of these questions to be addressed (Rutz & Hays, 2009).

The addition of sensors and memory capacity to telemetry devices, now termed 'bio-loggers,' allows for the direct *in situ* measurement of the animal's internal and external environment. This is perhaps best demonstrated by the deployment of CTDs on marine predators, enabling the autonomous collection of biological data from the perspective of the animal utilising the environment, and reducing the logistical cost of manually collecting the same data (Boehlert et al., 2001; Wilson et al., 2002; Hooker & Boyd, 2003). Researchers have since identified at least 24 different types of sensors and their potential applications to monitor the entire spectrum of an animal's biological life history from birth to death (Ropert-Coudert & Wilson, 2005). This integrative cooperation between physiologists, behaviourists and physical oceanographers places bio-logging at the forefront of a 21st century multidisciplinary approach to studying ecology (Block, 2005).

The term “bio-logging” was conceived in March of 2003 at the International Symposium on Bio-logging Science held at the National Institute of Polar Research (NIPR) in Tokyo, Japan, and refers to the “investigation of phenomena in or around free-ranging organisms that are beyond the boundary of our visibility or experience” Boyd, Kato, & Ropert-Coudert, 2004; Cooke et al., 2004; Naito, 2004). These bio-loggers archive a continuous time-series to an internal storage unit, no longer relying on the transmission of just a subset of the data to remote receivers, and allow ever larger datasets to be recorded (Boehlert et al., 2001). The first use of bio-logging devices occurred inadvertently decades prior when in 1940, Per Scholander (1940) published his measurement of the diving depth of a dying fin whale (*Balaenoptera physalus*) by equipping the harpooned mammal with a capillary tube originally used to take depth readings from the sounding lines of ships. The first purpose built bio-logger came years later and consisted of a Time-Depth-Recorder (TDR) adapted from a kitchen timer and a pressure sensor, and recorded on glass disks; profiling the diving bouts of Weddell seals (*Leptonychotes weddelli*) for up to one hour (Kooyman, 1965). Advances in solid-state technology have allowed for the miniaturisation of sensors and memory storage devices and enabled the production of current bio-loggers such as the ‘daily-diary’ tag that can record in 14 different channels for deployments ranging up to 105 days (Wilson, Shepard, & Liebsch, 2008).

The primary advantage of bio-logging to that of biotelemetry is that it is no longer necessary to maintain a communication link with the equipped animal for the transmission of data; allowing for the monitoring of deep-diving animals, long-ranging animals, or animals that are otherwise difficult to follow due to hazardous environments (Wolcott, 1995). The uncoupling of transmitter and receiver also increases the volume of data that can be obtained. Previous sensors that transmitted their data were limited by the bandwidth of satellite systems like ARGOS to transmitting just a subset or sample of their records (Whitney, Papastamatiou, & Gleiss, 2012). New limitations are consequently introduced as the internal archiving of data necessitates the recovery of these devices; a task that can be achieved through the coupling of bio-loggers with tracking beacons (Wolcott, 1995).

The availability of sensors for bio-logging applications renders such devices well placed for use in measuring indicators of the potential impacts to marine species of climate

change or the effect of anthropogenic water users (Boyd, Kato, & Ropert-Coudert, 2004). Cooke (2008) contends that the ability of bio-loggers to quantify measurements of behaviour, survival, spatial ecology, energetics, and physiology can provide an assessment of every biotic and abiotic threat to an endangered species. The large body sizes of apex predators and their role in the trophic structure of an ecosystem makes these species well suited for the deployment of bio-loggers as their status may serve as an indication of the health of their respective environments. Consequently, these megafauna have been the target of many recent bio-logging investigations, with most involving whales, seals, turtles, sharks or seabirds (Boyd, Kato, & Ropert-Coudert, 2004; Wilson et al., 2008). The accelerometer is one such bio-logging sensor that can be used to reveal in finer detail what an animal is doing along its movement trajectory (Yoda et al., 1999).

ACCELEROMETERS

Acceleration is the rate at which velocity changes with respect to time. Velocity is a vector quantity having both a magnitude and a direction, and thus acceleration describes both the rate of change in speed and also any change in direction, and is usually measured in $m.s^{-2}$ (Crew, 1908). In its simplest form, an accelerometer consists of a seismic proof mass suspended or counter-balanced by a dampened spring, the displacement of which corresponds to the linear inertial acceleration imparted on the device enclosure, and through the spring, on the mass (Norton & Warner, 1921). Modern solid-state accelerometers can convert this mechanical displacement to an electrical signal using the piezoelectric, piezocapacitive, or piezoresistive properties of an element. In the case of piezoresistance accelerometers, the sensor is a micro-etched integrated circuit supporting a silicon cantilevered beam that widens to a paddle shape and supports a dense proof mass. The beam acts as the mechanical spring and a resistor is placed across the beam so that acceleration of the proof mass flexes the beam and changes the electrical resistance in proportion to the acceleration (Roylance & Angell, 1979). This form of accelerometer measures linear acceleration in one axis. By incorporating two other sensors orientated perpendicular to one another, motion in all three axes can be detected.

The accelerations measured by these devices are termed proper accelerations, that is, acceleration relative to a local inertial frame of reference. This differs from the true rate

of change in velocity, called coordinate acceleration, as the frame of reference, the observer, is not fixed in a coordinate system such as the surface of the Earth, but is travelling with the sensor as the housing of the device. Proper acceleration measured by an accelerometer exists in the frame of reference of the device, and in this case the inertial frame of reference is called the free-fall reference frame (Einstein, 1920). It is necessary to clarify this difference; a body in free-fall appears to accelerate at 9.8 $m.s^{-2}$ from the perspective of an observer on the surface of the Earth, however an accelerometer placed on the same body will read an acceleration of 0 $m.s^{-2}$ as it is not accelerating with regard to the frame of reference against which it is measured – the body in free-fall. As a result, an accelerometer cannot directly measure the apparent acceleration of gravity during free-fall; an accelerometer at rest on the surface of the Earth will however measure 9.8 $m.s^{-2}$, the acceleration due to gravity, but only through the mechanical interaction of the device with the upward ground reaction force of the Earth resisting free-fall. To distinguish proper acceleration from coordinate acceleration, units of G are used, where 1 G is equivalent to standard Earth gravity or 9.8 $m.s^{-2}$.

Einstein's equivalence principal also stipulates that linear acceleration, that is acceleration due to dynamic motion, is indistinguishable from gravitational acceleration (Einstein, 1920). Thus static acceleration caused by the position of a body in relation to gravity, and dynamic acceleration caused by the movement of a body cannot be differentiated by an accelerometer. However, a running mean or band-pass filter can be used in order to separate the generally low frequency components of static acceleration from the high frequency components of dynamic motion, allowing for the calculation of posture with reference to gravitational acceleration (Shepard et al., 2008; Wilson et al., 2008).

Accelerometers present some useful advantages for use in detecting motion when compared to other methods like the Hall sensor or electromyogram (EMG) sensors, in that accelerometers have the ability to measure not only the frequency of movements, but also their amplitudes (Kawabe et al., 2003b). The ability of the accelerometer to also measure gravitational acceleration and in turn the derivation of posture is yet another benefit not found in other sensor types (Tanaka, Takagi, & Naito, 2001).

Rutz and Hays (2009) contend that the recent development of analytical tools for the study of energetics and behaviour, has contributed to the rapid interest in accelerometer applications. Data-loggers are being deployed increasingly on humans and animals for the study of locomotory patterns as a direct result of the accelerometer's ability to measure movement. Quantification of movements in the surge, sway, and heave axes can provide a useful means for detecting behaviour (Yoda et al., 1999; Kawabe et al., 2003a; Watanabe et al., 2005), quantifying energy expenditure (Williams et al., 2004; Wilson et al., 2006; Halsey et al., 2008), and making other conclusions with regard to the physiology of study specimens (Nowacek et al., 2001; Watanuki et al., 2003; Watanabe et al., 2006). What follows is a review of some of the analytical tools and innovations presented by accelerometry.

ETHOGRAPHER

Early deployments of accelerometers for the study of behaviour relied on visual inspection of the time-series for analysis (Yoda et al., 1999). This method requires some form of annotation so that the time-series may be ground-truthed to real observations. Real-time narrative annotation can prove difficult due to sampling decisions made by the observer when a continuous record of behaviour is not available; subjectivity, limitations of visibility, or the timing of observations are but a few factors that can limit observations (Altmann, 1974). Video offers a method for preserving the observational record for later coding and removes the need for the observer to make critical sampling decisions that may introduce an unnecessary bias (Noldus et al., 2000). Others have used decision trees based on the accelerometer signature to differentiate between behaviours (Gómez Laich et al., 2008; Gleiss, Gruber, & Wilson, 2009). Visual inspection of the accelerometer time-series still requires some familiarity with the physics behind the device; a truly autonomous approach would serve to remove any observer bias in interpreting the data. Watanabe et al. (2005) experimented with the efficacy of using a Fast Fourier Transform (FFT) and Power Spectral Density (PSD) to identify the dominant frequency within particular movements, and subsequently passing this and four other parameters onto a stepwise Canonical Discriminant Analysis (CDA) to categorise different behaviours (Watanabe et al., 2005). This method also has limitations as prior knowledge of the species is necessary to identify the behaviours being discriminated by the device.

Ethographer is a software package built upon the IGOR Pro platform (WaveMetrics, Lake Oswego, OR), designed for the analysis, transformation, visualisation, and presentation of bio-logging data. The wave and mask analysis tools provide users the ability to extract behavioural patterns from accelerometer time-series data. Categorisation via the wave analysis tool is accomplished by performing a spectral analysis of the data by continuous wavelet transformation, followed by an unsupervised k-means clustering algorithm (Sakamoto et al., 2009). The wavelet transform is similar to a windowed FFT in that it decomposes a signal into its composite frequencies, but differs in its basis functions. FFT defines a signal using sine and cosine functions, whereas wavelet analysis has the ability to use more complex 'mother wavelets' which can be designed for improved resolution by including properties like long, low-frequency windows while simultaneously including short, high-frequency windows (Graps, 1995). After transformation, the frequency spectra are subjected to a k-means clustering algorithm, which assigns the data to a pre-defined number of random centroids. The centroids are then recalculated based on the clusters and repartitioned until some criterion of convergence is met (Jain, Murty, & Flynn, 1999).

Ethographer allows for the automated classification of accelerometer data without a prior ethogram of the species. To test the effectiveness of this application, Sakamoto et al. (2009) ran the analysis on accelerometer time-series of European shags (*Phalacrocorax aristotelis*). Four parameters needed careful selection based on the characteristics of the study species; cycle range, corresponding to expected dynamic body accelerations of the study species, the number of behavioural patterns to cluster, a wavelet sensitivity parameter to describe the mother wavelet and adjust the sensitivity of the transformation to time and periodicity, and a final parameter defining the minimum duration of the behaviours to be identified. Some patterns with similar spectra were identified as a result of overestimating the number of clusters to identify and were simply combined when deemed appropriate. Several clusters were also identified that included walking and running behaviours, due to the gradual transition of periodicities between the two movement patterns. The authors note that their use of only surging acceleration may have limited the ability of the analysis to differentiate between certain behaviours, and incorporation of further sensors, body posture, or GPS

would help to complete the ethogram, but the method still presents a novel procedure for analysis of accelerometer data (Sakamoto et al., 2009).

The mask analysis tools allow a method for behavioural categorisation by providing the user with an interface to the IGOR Filter Design Laboratory (IFDL; WaveMetrics, Lake Oswego, OR) and mask calculation tools. These tools allow the design of filters that extract specific elements of the acceleration record and allow the creation of masks that categorise the record by logical 'on/off' values. Okuyama et al. (2009) utilised Ethographer to identify breathing and feeding behaviours from the acceleration signal recorded by a data-logger attached to the lower beaks of loggerhead turtles (*Caretta caretta*). By using Ethographer's IFDL interface to filter accelerometer records, they successfully identified 99.6 ± 1.1% (mean ± S.D.) of feeding activities and 100% of breathing activities. The false detection rate was 24.8 ± 12.4% for feeding behaviours and 2.4% for breathing behaviours. Naito et al. (2010) similarly used the mask calculation tools to isolate feeding events from mandibular acceleration data of Weddell seals by applying combinations of filters to the dominant cycle, dominant amplitude, and duration components of each signal. With this method, the researchers achieved a feeding behaviour detection rate of 89.8 ± 13.5% and a false detection rate of 25.9 ± 10.9% (Naito et al., 2010). This method requires some knowledge of the study species to initially define the parameters of the band-pass filters for the extraction of specific behaviours, but serves to further demonstrate some of the analytical capabilities of the Ethographer software.

Ultimately, these tools offer innovative methods for developing ethograms and identifying behaviours. With previous knowledge of the study species, the toolset can extract specific movements from a record of accelerations. If there is no prior knowledge, accompanying video data, or annotation, the software nevertheless has the potential to identify different patterns that may not have been observed previously, or to identify patterns that can be later identified (Sakamoto et al., 2009).

Accelerometry in Marine Animals

The first study to assess patterns of swimming by measuring acceleration of marine animals was published in 1976, but relied on instruments tethered to computers by data-transmitting cables (DuBois, Cavagna, & Fox, 1976). In this study, the

hydrodynamics of shad (*Pomotamus saltatrix*) locomotion were investigated, revealing different patterns of symmetric and asymmetric acceleration corresponding to different swimming speeds. DuBois & Ogilvy (1978) later utilised accelerometers and pressure transducers to calculate the power and efficiency of the shad tail by comparing the forward and lateral force of water on the tail from the pressure transducers, with the forward and lateral force on the body calculated from acceleration. These studies provided exciting new methods to analyse the mechanics of swimming fish, but could not be tested on free-swimming individuals due to the limitations of the cable connection.

A brief interest in the use of accelerometers for the study of swimming kinematics soon followed. Freadman (1981) explored the use of accelerometers and metabolic measurements to determine the energetic costs of switching between active brachial and ram gill ventilation in bluefish and striped bass (*Morone saxatilis*) using estimations of swimming drag from body acceleration. He found no drag-associated increase in acceleration when fish adopted ram ventilation. This was attributed to turbulence caused by active ventilation that is smoothed along the body when switching to ram ventilation, effectively reducing drag (Freadman, 1981). Sharks also switch between buccal pumping and ram ventilation, though some pelagic species have lost the former ability and are obligate ram ventilators (Roberts, 1975).

Stroke Rate and Tail Beat Frequency (TBF)

The deployment of accelerometers quickly proliferated throughout a range of large marine organisms following the miniaturisation of the data-loggers, allowing for the development of many analytical techniques for exploring the locomotory patterns and energetics of marine species. In one such deployment, adult Adélie penguins (*Pygoscelis adeliae*) were fitted with accelerometers and the lateral acceleration records used to determine wing beat frequency (Arai et al., 2000). By applying a spectral analysis in the form of a FFT to acceleration data, power spectrum density (PSD) could be calculated to identify the dominant frequency in the signal. During descent, when penguins were actively propelled by wing beats, the cycle identified by PSD corresponded well with wing beat frequency. Arai et al. (2000) suggested that further comparative analysis with other species may be important for analysing very high-frequency kinematic data. Kawabe et al. (2003b) deployed similar devices on rainbow trout (*Oncorhynchus mykiss*)

to confirm the relationship between tail beat activity and acceleration frequency. A reliable measurement of tail beat activity can then be used to estimate energy expenditure and cost of transport. Kawabe et al. (2003b) noted the ability of accelerometers to measure low frequency tail beats, which is useful for calculating instantaneous speed when a fish is swimming below the stall speed of water speed sensors.

Quantifiable observations of TBF can then be used to draw further conclusions regarding animal behaviour and physiology. Davis et al. (1999) used sway axis from accelerometers on Weddell seals to determine flipper stroke frequency. This information was used in conjunction with video footage and other data recordings to identify swimming strokes and thus locomotory activity while foraging. During one event, a change in flipper stroke frequency was used to infer that a seal had visually located and was beginning to pursue a prey item. Although circumstantial, this evidence helps to establish the concept that different swimming patterns may be identified by their different stroke rates. A similar technique might be used to identify changes in shark swimming patterns, such as the burst swimming events observed in some sharks preceding prey capture (Martin, Hammerschlag, Collier, & Fallows, 2005) or as hypothesized for sharksucker (*Echeneis naucrates*) removal (Ritter & Brunnschweiler, 2003).

A deployment on Weddell seals concluded that thinner seals adopted a gliding dive strategy whereas fatter seals used a stroke-and-glide swimming pattern (Sato et al., 2003). The gliding strategy proved to be more efficient based upon the time seals spent recovering at the surface between dives. These results provide further evidence for the ability of accelerometers to identify swimming patterns by measuring stroke frequency of underwater animals. Williams et al. (2004) expanded upon these conclusions and introduced the potential for accelerometers to estimate energy expenditure by calculating the per-stroke energetic cost of diving seals as part of a larger approximation of total energetic cost in pinnipeds. Their results, collected by using accelerometers in conjunction with an open-flow respirometer, indicated a linear relationship between oxygen consumption and the number of strokes made by diving seals. Although there are many factors that contribute to the total energetic cost of a given animal, including basal metabolic rate, thermoregulatory costs, and digestive

costs, there is a selective advantage for individuals that can reduce their locomotory costs (Weihs, 1974, Au & Weihs, 1980, Williams et al., 2000). The use of accelerometers to calculate per-stroke transportation costs has the potential to reveal much about the energetic budget of sharks, some of which are thought to require constant movement as obligate ram-ventilators (Roberts, 1975).

Quantification of TBF via the accelerometer data-logger allows for the *in situ* observation of frequency and amplitude of flipper and tail strokes in marine species, a measurement not afforded by other methods like tail-beat indicators and video recording. This precision allows scientists to draw further conclusions with regard to the locomotory patterns of their study species, making inferences of such aspects as behaviour, buoyancy compensation, and energetics.

Pitch and Body Angle

Einstein's (1920) equivalence principle shows that gravitational acceleration is indistinguishable from dynamic acceleration. Estimation of the gravitational component of acceleration can be achieved however, by separation of the static signal from the dynamic signal through smoothing via a running mean (Shepard et al., 2008) or processing through a low pass filter (Tanaka, Takagi, & Naito, 2001). Static acceleration values range from +1 G to -1 G; when any one of the accelerometers three axes is aligned with the gravitational field of Earth, that axis will read +1 G when orientated upwards, opposite the gravitational field and -1 G when orientated downwards. The amplitude of static acceleration in the surge axis thus reflects the degree of inclination of the accelerometer with respect to the Earth's gravitational field and can be used to estimate the pitch of a tagged animal, as illustrated in penguins (Yoda et al., 2001). Changes in static acceleration of the heave axis can also be used to determine body pitch. Because the conversion from acceleration to body angle is an arcsine function, calculations from the surge axis are most sensitive to changes of inclination between 0° to 45° and 135° to 180°; those from the heave axis are most sensitive in the 45° to 135° range. This sensitivity is a result of the proportionally greater change in amplitude of the respective axis within the specified range (Shepard et al., 2010).

Nowacek et al. (2001) used a multi-channel data-logger to investigate buoyancy and diving behaviour of North Atlantic right whales (*Eubalaena glacialis*) in the Bay of

Fundy. By analysing pitch angle as determined from the accelerometer channels of the device during diving and ascent, they showed that right whales are positively buoyant at the surface. This insight into the swimming efficiency of whales further demonstrates the ability of accelerometers to reveal important information beyond that of describing behaviour. Ship collisions are a leading cause of anthropogenic mortality in whales (Laist et al., 2001) and the fact that right whales are positively buoyant at the surface may help provide new management strategies for their conservation (Nowacek et al., 2001). By calculating pitch angle, accelerometer data could detect individual fluke strokes on northern right whales and sperm whales (*Physeter macrocephalus*). Scientists used this ability to quantify a whale's reaction to a suite of noises including sonar, passing ships, and socialising whales (Johnson & Tyack, 2003).

Estimations of body angle were also used to make inferences of foraging strategy in macaroni penguins (*Eudyptes chrysolophus*; Sato et al., 2004). Here, a significant correlation between body angle and bottom time was observed and thought to suggest that penguins ascend steeply and quickly after encountering a prey patch and depleting their oxygen stores, but ascend gradually at a shallow angle when no prey is encountered, using the ascent to search for more productive grounds (Sato et al., 2004). Body pitch can be an indicator of foraging behaviour in sharks such as the scalloped hammerhead that has been observed to make sharp dorsal turns to pick up food from the surface of the seafloor (Nakaya, 1995). Foraging behaviour of similar species can then be directly quantified *in situ* by using accelerometer data-loggers to estimate body pitch.

Swimming Patterns and Behaviour

Measures of TBF and body angle can then be used to more explicitly quantify swimming behaviours. Yoda et al. (1999) identified porpoising behaviour in penguins equipped with two-axis accelerometers and depth sensors based on a specific acceleration pattern in the surging axis. In 2001, the authors were able to expand on this method, differentiating between walking, tobogganing, standing on land, lying on land, resting at the water surface, porpoising, and diving by using an automatic classification based on the posture derived from the acceleration waveform, and a manual inspection of the data (Yoda et al. 2001).

Kawabe et al. (2003a) described the use of an accelerometer to characterise different behaviours in Japanese flounder (*Paralichthys olivaceus*). After ground-truthing with video footage, they used acceleration signatures, in addition to data from speed and depth recorders, to successfully identify active swimming, inactive gliding, bottom-burying, and bottom-resting behaviours in captive flounder. Swimming and burying behaviours were determined exclusively from the accelerometer by identifying dominant frequencies from a FFT of the data. The results of this study help to reaffirm those of Yoda et al. (2001) in establishing the accelerometer as a practical tool for the measurement of tail beat activity and quantification of behaviour. Such studies demonstrate that specific behaviours and swimming patterns can be inferred from estimates of body angle, TBF and amplitude from accelerometer data. As researchers became more familiar with the device and analysis techniques, higher order behaviours could be distinguished. This was illustrated in chum salmon (*Oncorhynchus keta*) when Tsuda et al. (2006) were able to distinguish between swimming, nosing, exploratory digging, nest digging, nest probing, oviposition, nest covering, and post-spawning digging behaviours by defining threshold values in both the posture and tail beats of instrumented fish. Similar results were recorded in free-living imperial cormorants (*Leucocarbo atriceps*), where standing, sitting, floating, flying, walking and diving activity patterns were differentiated by processing static and dynamic acceleration records through a simple decision tree analysis (Gómez Laich et al., 2008). Accurate quantification of free-ranging behaviour allows for the creation of detailed time-budgets and can help to reveal information on foraging strategies; such as in Cape gannets (*Morus capensis*), which were found to forage in phases upon reaching prey patches, perhaps as a strategy to recover transportation costs (Ropert-Coudert et al., 2004).

The first use of an accelerometer on a shark was reported in 2007 (Whitney et al., 2007). In this study, diel activity patterns were revealed in captive whitetip reef sharks (*Triaenodon obesus*) by using two-axis accelerometers to detect periods of activity and inactivity. Movement was inferred when the logger was towed horizontally by the shark, compared with periods of inactivity when the logger floated vertically in the water column. This pioneering study offered a reliable method for simple long term movement studies, but its failure to use the accelerometer to its full potential limits its ability to detect the fine scale movements necessary to truly assess behaviour and

swimming patterns. The authors suggested a multi-point attachment method to increase logger sensitivity.

In 2009, a team from Swansea University reported the tagging of two captive Lemon Sharks (*Negaprion brevirostris*) in the Bahamas (Gleiss, Gruber, & Wilson, 2009). Researchers first calibrated tri-axial accelerometer data with synchronised video recordings of tagged individuals to establish threshold acceleration levels for each of four swimming patterns; resting, initiation of swimming, steady-swimming, and fast-start swimming. They then successfully used TBF and amplitude in a hierarchical decision tree to differentiate between the swimming patterns. Though the behaviours identified are basic and uncomplicated, they serve as the foundation for higher order actions like prey ambush and mating. This study further established the ability of accelerometers to reveal much about the behavioural ecology of sharks, provided a wide range of behaviours can be observed during ground-truthing.

Another study coupled accelerometers with animal-attached cameras to determine whether the 'yo-yo' diving behaviour observed in tiger sharks (*Galeocerdo cuvier*) is associated with optimising transport efficiency or with prey hunting behaviour (Nakamura et al., 2011). The team used Ethographer to generate spectrograms and cluster similar spectra. Analysis of the accelerometer data revealed that gliding dives occurred infrequently, with powered swimming being observed more often in descents. This contradicts previous predictions that negatively buoyant sharks conserve energy by gliding during descent (Weihs, 1973). One tagged shark made dives below the thermocline, perhaps an indication of thermoregulation such as that observed in tuna (Holland et al., 1992). Fast-start swimming events observed in the acceleration data, coupled with the presence of prey items in image data, suggest that 'yo-yo' diving may be a foraging strategy. A vertical movement hunting strategy would be in accord with the Lévy-like movement frequencies that optimise prey location in patchy distributions (Sims et al., 2008). The authors suggest that this method would also coincide with the observation that many sharks utilize a number maximisation foraging strategy (Bres, 1993), as 'yo-yo' diving would help to increase encounters with prey. Navigation cannot be precluded as a possible impetus for 'yo-yo' diving, but the visual presence of prey items lends credence to the optimal search strategy theory. Coupled with visual

observation, the field of accelerometry has the capacity to reveal the motivation for a wide range of behaviours.

As a final example, Whitney et al. (2010) revisited their use of the accelerometer data-logger in an investigation into the behaviour of free-swimming nurse sharks (*Ginglymostoma cirratum*), categorising resting in still water, resting in a surge zone, steady-state swimming, fast-start swimming, and mating swimming patterns. In this experiment, scientists anchored the accelerometer to the base of the second dorsal fin and used Ethographer to perform a spectral analysis and to cluster similar behavioural spectra, which could be compared with field observations to describe the clustered behaviours. Using this method, they classified 26 mating events, confirming two by direct observation. This study represents a novel method for quantification of mating behaviour in sharks, an otherwise difficult event to observe in the field. Mating has been observed directly in only a few species of sharks, but it is suggested that the behaviour is conserved among different species (Bres, 1993). Regardless of this assumption, the authors suggest that the movements associated with mating in sharks will produce distinct acceleration patterns that can be easily identified (Whitney et al., 2010). Further observation of nurse sharks, and other species will help to reveal more about their reproductive behaviour, and ultimately lead to the identification of mating grounds; a vital step for species conservation.

Overall Dynamic Body Acceleration

The contraction of skeletal muscle required for animal movement is governed by various kinematic factors, but fundamentally initiated by the expenditure of the biological energetic currency, adenosine triphosphate (ATP; King, Loiselle, & Kohl, 2004). Measurement of movement should thus provide an estimate of the energetic cost required for its generation. Given that accelerometers are well suited for the quantification of animal movement, they should also provide an accurate estimate of the rate of energy expenditure required for locomotion (Wilson et al., 2006). Acceleration has been shown to correlate well with energy expenditure in humans, measured by indirect calorimetry and respirometry under laboratory conditions (Meijer et al., 1989; Bouten et al., 1994). This concept was also introduced in animals with the measurement of per-stroke energetic costs of swimming in seals, although the calculations were based only on the frequency of strokes, ignoring stroke amplitude (Williams et al., 2004). The

ability of whole body movement, as measured by tri-axial accelerometers, to predict energy expenditure was formally tested in captive great cormorants (*Phalacrocorax carbo*) and free-living imperial cormorants while the birds demonstrated different activities in the laboratory and in the field. In this experiment, dynamic movement was differentiated from gravitational acceleration by smoothing the accelerometer record over 1 s intervals and subtracting this from the unsmoothed record. The absolute positive values of these units from all three axes were then summed to provide a measure of overall body movement, termed Overall Dynamic Body Acceleration (ODBA). Here, ODBA showed a significant positive association with oxygen consumption, an indirect measure of energy expenditure (Wilson et al., 2006). These findings, together with data from humans (Halsey et al., 2008), highly active animals (Elliot et al., 2013) and comparatively inactive animals (Green et al., 2009), confirm the potential for tri-axial accelerometers to estimate energetic costs in free-living animals (Wilson et al., 2006). Thus accelerometers can provide estimates of field metabolic rate similar in power to doubly-labelled water and heart rate techniques but without their temporal and physiological limitations (Butler et al., 2004; Elliot et al., 2013). The theory and methodology behind this approach has since been tested on a range of species, finding similar results within species groups (Halsey et al., 2009; Gleiss, Wilson, & Shepard, 2011).

The first test of this relationship for fish was conducted on juvenile scalloped hammerhead sharks. Partial Dynamic Body Acceleration (PDBA), the calculation of dynamic movement in only two axes, was shown to correlate with energy expenditure during steady-swimming. Sharks exercised in a respirometer revealed a linear relationship between PDBA and metabolic rate, though extrapolation to sharks swimming erratically in a pond or tank resulted in metabolic rates that were not biologically feasible. In this case, extrapolation of log transformed data provided more realistic or plausible results. This discrepancy may be attributed to flaws in the experimental design, including the limited range of swimming speeds that researchers could elicit from sharks in the respirometer (Gleiss et al., 2010). Nevertheless, this study introduced prospective new metrics for activity-specific energy expenditure in fish and demonstrated the need for further experimentation. A similar study investigated the relationship between acceleration, heart rate, TBF, and energy expenditure of adult

sockeye salmon (*Oncorhynchus nerka*) in a swim tunnel respirometer (Clark et al., 2010). It found a similar linear relationship between energy expenditure and activity as derived from the accelerometer, although in this case gravitational acceleration was separated from the overall measurement of activity (Clark et al., 2010).

Given the ability of accelerometers to estimate *in situ* energy expenditure, we can begin to quantitatively test movement strategy hypotheses. Gleiss, Norman, and Wilson (2011) deployed accelerometers on whale sharks to model dive geometry by measuring trajectory and locomotory activity. They compared the cost of transport (COT) of dives at varying pitch angles by using PDBA as a proxy for energy expenditure. Their results suggest that whale sharks utilise different dive strategies to minimise COT in either the horizontal or vertical dimension, perhaps in response to ecological factors (Gleiss, Norman, & Wilson, 2011). With further study, accelerometers may have the potential to reveal dive function in sharks; discriminating between hunting dives, foraging dives, orientation dives, and travel dives.

CHAPTER 2. IDENTIFICATION OF COMMON SMOOTHHOUND SHARK SWIMMING BEHAVIOUR FROM TRI-AXIAL ACCELEROMETER DATA

INTRODUCTION

Many populations of sharks currently face risk of extinction due to pressures of overexploitation. The International Union for the Conservation of Nature (IUCN) currently recognizes 20 species of pelagic sharks and rays as either vulnerable or endangered; nearly 32% of the 64 species covered by the report (Camhi et al., 2009). Of the 1,045 species of sharks, skates, and rays assessed globally, 17% are listed as Threatened, and 47% as Data Deficient, a reflection of current fishing practices and an indication of a general absence in knowledge of shark movement patterns, population trends, and the role they play in the marine ecosystem. Empirical and theoretical evidence suggests that the loss of shark populations can result in complex changes to community structure that cascade through trophic and behavioural interactions (Ferretti, et al. 2010). Ocean use guidelines and shark culling programs that arise periodically following shark attacks are often based on assumptions of shark movement and foraging strategies (Meyer et al., 2009). In both cases there are few concrete data, as the movement ecology, and the intricate ecological roles that sharks play are only beginning to be studied. It is for these reasons that there is a pressing need for further research and understanding of these predators.

The field of biotelemetry offers one means to reveal much about the physiology, behaviour, and energetics of free-ranging animals (Chapter 1). The most basic and most widespread approach is the spatial and temporal quantification of animal movement (Cooke et al., 2004). Knowledge of position and movement can allow scientists to make indirect inferences with regard to behaviour, ecology, and social interactions of an animal (Rutz & Hays, 2009). Bonfil et al. (2005) reported the discovery of a large-scale movement of a great white shark after satellite tracking revealed a transoceanic journey from South Africa to Australia. Tracking studies such as these have important implications for the conservation and management of marine species, and serve to fill the current void in the understanding of elusive and charismatic species like the white shark.

Increasingly however, researchers are searching for higher resolution movement data. Scientists want to know what occurs along these migrations; how animals pursue prey, interact, and navigate (Rutz & Hays, 2009). Bio-logging offers a way to answer these questions. Locomotory activity, ventilation, heart rate, blood pressure, and thermal properties are just a sample of the spectrum of variables that can be measured and recorded remotely with devices like accelerometers, pressure transducers, ultrasonic Doppler sensors, electrodes, and thermistors (Cooke et al., 2004). Bio-logging thus has the potential to reveal information on physiology, behavioural ecology, spatial ecology and energetics, all of which have large implications for conservation. In addition to providing essential information to better understand those animals that have been classified by the IUCN as Data Deficient, Cooke (2008) contends that bio-logging has the capacity to quantify every criterion required to classify a species' threat status.

One such bio-logging device is the accelerometer, which measures orientation and body movement by detecting changes in velocity (Chapter 1). Animal movement, often a representation of animal behaviour in response to environmental and physiological conditions, can be quantified with an accelerometer (Shepard et al., 2010). However, with the development of new analytical techniques there comes a pressing need for calibration experiments to test their applicability to field research. The scope of this experiment is a ground-truthing of the accelerometer for the description of behaviour in captive swimming common smoothhound sharks.

The common smoothhound shark (*Mustelus mustelus*; Linnaeus, 1758) has a geographic distribution from the Mediterranean and eastern Atlantic to southern Africa. Common smoothhounds are a shallow-water, bottom-dwelling, coastal species of the continental shelf and upper slope, often caught in less than 100 m of water, and feeding mainly on crustaceans and polychaetes, and cephalopods (Compagno, 1984; Smale & Compagno, 1997).

All sharks exhibit characteristics of the K-selected life strategy; slow growth, late sexual maturity, long life expectancy, low fecundity, low natural mortality, and the production of small litters of offspring. This presents a unique situation when compared with r-selected teleosts, as shark populations may take many generations to recover from

anthropogenic threats of overfishing, habitat destruction, and pollution (Camhi et al., 2009; Stevens, Bonfil, Dulvy, & Walker, 2000).

Smoothhound sharks are usually retained as a bycatch species in both the hake trawl and longline fisheries. Sharks also are taken opportunistically by the commercial line fishery when teleost species are either uncatchable or prices too low, as prices for sharks are only one third that of teleosts. Smoothhound sharks are probably one of the dominant species of sharks and rays landed in the commercial line fishery around South Africa (Smale, 1997).

At present, the IUCN lists the common smoothhound as Vulnerable, citing unsustainable catches in South Africa as a justifying factor (Serena et al., 2004). A stock assessment performed by da Silva (2007) suggested that catches were up to 2.5 times higher than recruitment in some parts of South Africa, and that catches must be halved in order to ensure sustainable exploitation.

This project deployed accelerometers for the indirect detection of behaviour in captive common smoothhound sharks. The objective of the study was to evaluate different methods of extracting swimming patterns from the accelerometer data. These methods included (i) manual interpretation and annotation of the accelerometer record, and (ii) autonomous annotation of the accelerometer record by classification based on a spectral analysis of the record. The accuracy and computation times for each method of extracting swimming patterns from accelerometer data were investigated and compared. Within this framework, I sought to investigate if tail beat frequency or swimming behaviour was independent of quantification method; be it visual quantification from direct observation in the form of video recordings or indirect quantification of acceleration signals recorded by data-loggers. I hypothesised that estimates of TBF would not differ between visual quantification and automated computer quantification, and that time timing and duration of four swimming behaviours (steady swimming, gliding, resting, and burst swimming) would also not differ between visual quantification from *in situ* observations, manual annotation of the accelerometer record, or automated annotation by Ethographer.

METHODS

STUDY SITE

The Shark Lab in Mossel Bay is an African Association of Zoos and Aquaria (PAAZAB) member aquarium that houses a 7.1 x 2.3 x 2.1 m shark tank. The tank is circulated with 35,000 l of natural, filtered seawater changed daily from the ocean, and experiences annual temperature fluctuations of 17.8 to 26.0°C, reflecting the natural seasonal oscillations of the area.

DEVICE

The HOBO® Pendant G data-logger (UA-004-64, Onset Computer Corporation; Figure 1) is a capacitive accelerometer with the ability to measure acceleration in three axes with a range of ±3 G (29.4 $m.s^{-2}$) at a resolution of 0.025 G (0.245 $m.s^{-2}$) and with an accuracy of ±0.075 G (0.735 $m.s^{-2}$) at 25°C and ±0.105 G (1.03 $m.s^{-2}$) from -20°C to 70°C. The data-logger is packaged in a waterproof housing, weighs 18 g in air and measures 58 x 33 x 23 mm (sectional area 7.6 cm^2). Its memory capacity of 64 kB allows the data-logger to record for 1 hour and 12 minutes at 5 Hz recording frequency. Data-loggers are factory calibrated to units of G.

DATA COLLECTION

Five specimens of common smoothhound (Table 1) were captured from Mossel Bay, South Africa during 2012 using rod and reel with baited circle hooks. Upon capture, the sharks were transported to the Shark Lab for acclimatization in a covered rectangular container containing natural seawater. At the Shark Lab, seawater from the display tank was dripped into the transfer bucket containing the shark until the pH level in the transfer bucket matched that in the tank. While in captivity, the sharks were fed a diet of thawed fish, squid or crab three times weekly, and housed for a maximum of three months. Newly caught sharks were provided two weeks to acclimate to the tank before experimentation began and did not undergo testing until they readily accepted food in captivity. Only specimens weighing greater than 1000 g were tested so that the 18 g mass of the logger was never more than 2% of the animal's body weight. Selection of larger sharks also reduced the proportion of drag introduced by the frontal area of the logger, as did caudal attachment of the logger (Bannasch, Wilson, & Culik, 1994). Wilson and McMahon (2006) highlight the importance for monitoring the impacts of device and restraint induced stress for improving the biological relevance and ethics of tagging

studies. One individual (No. 5, Margarita) instrumented in this study displayed swelling and discolouration in the area of the tag placement, indicating a possible stress response to tagging.

Table 1. Details of individuals used in experimental deployments. TL: Total Length at capture. A total of 5 sharks were tagged with accelerometers for a collective duration of 28 hours.

No.	Nickname	Sex	TL (cm)	Weight (g)	Duration (h)
1	Scarface	F	85	3380	5.2
2	Pansy	F	97	3000	3.2
3	Lola	F	65	1140	7.7
4	Monica	F	100	2400	6.5
5	Margarita	F	73	1600	5.4
				Total	28.0

Figure 1. HOBO Pendant G data-logger. Note the orientation of the 3 perpendicular axes. Devices were orientated such that the X axis recorded acceleration in the surge axis, the Y axis sway, and the Z axis heave.

It was necessary to synchronise the visual observations and data logger to a common time scale. After starting the data-logger, it was filmed in front of a laptop display running stopwatch software (Xnote Timer v1.11, dnSoft Research Group) while rotating the logger 90° about the sway axis; a movement which could be distinctly identified in the accelerometer signal. The stopwatch software displayed time in tenths of a second, and this event provided a synchronisation of data-logger time with stopwatch time.

To prepare for deployment, sharks were recaptured in the aquarium by a trained diver and restrained underwater for device attachment in a natural state of paralysis (Henningsen, 1994). Tonic immobility, also known as animal hypnosis, is achieved in sharks by placing them in an inverted posture until they reach a state of torpor, and has been used with sharks as a technique for captive husbandry or for performing medical techniques (Henningsen, 1994). The time taken by the diver to capture the shark and attach the logger was recorded for each deployment and is termed Capture Time later in this text.

A fin clamp attachment method similar to that used by Heithaus et al. (2001) was originally tested, however airline tubing within the swimming enclosure presented some difficulties as the tag would repeatedly get snagged or tangled. For this reason a strap attachment was used. Data-loggers (Figure 1) were mounted to an elastic strap that was wrapped around the shark's trunk. The elastic material of the strap ensured the logger was held firmly against the body while providing enough flexibility to prevent the inhibition of movement. The data-loggers were positioned ventrally, anterior to the pelvic fins, such that the Y-axis of the device recorded lateral movement, or sway, the X-axis surge, and the Z-axis heave (Figure 2). The attachment occasionally failed resulting in the strap slipping from the trunk of the body. Deployments where this occurred were discarded from the analysis.

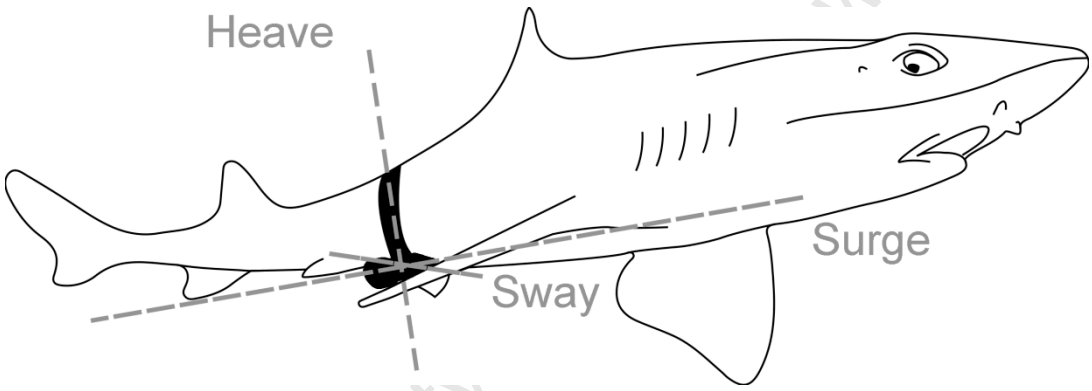

Figure 2. Diagram showing tag placement and orientation of data-logger axes.

Following attachment of the elastic strap, each shark was then filmed as it swam freely within the tank, beginning each video by recording a few seconds of the stopwatch to effectively synchronise the video frames with the stopwatch time. Previous studies allowed instrumented animals to recover and acclimate to the fitted device for periods ranging from 4 hours to 1 week (Tanaka, Takagi, & Naito, 2001; Kawabe et al., 2003b; Whitney et al., 2007; Kawatsu et al., 2010). However, due to the non-invasive attachment method and the small memory capacity of the logger device, this study began as soon as the shark was released back into the tank.

Members of Oceans Research internship program provided logistical support during the study. In order to minimise multiple observer bias, each observer was trained prior to and supervised during their observation period by the author. During the deployment, two observers monitored the focal shark carrying the datalogger throughout the 1 hour

and 12 minute deployment, recording changes in behavioural state and posture from an observation window at the end of the tank. The time and duration of four behavioural states were recorded, similar to those reported in lemon sharks (Gleiss, Gruber, & Wilson, 2009): steady swimming, defined by regular, rhythmic tail beats; gliding, defined as movement with the absence of tail beats; stationary resting, defined by the absence of tail beats or movement; and fast-start or burst swimming, defined by one or more quick tail beats followed by a sudden increase in swimming speed. The postural state of the shark was recorded as inclined, neutral, or declined, with neutral swimming defined as an attitude estimated visually between +45° to -45°, and inclined and declined swimming classified above and below this window, respectively. In some deployments, food was introduced or divers entered the tank to induce feeding and escape responses. In addition to experimental deployments, two types of control deployments were also performed. As a baseline control, un-instrumented sharks were observed swimming without interference from divers. For a stressed control, sharks were put through the motions of capture and tag attachment, but allowed to swim unimpeded by removing the tag before observation. Sharks performed a maximum of 3 deployments on a given day, and usually some combination of control and experimental deployments.

Data Analysis

A trained diver re-entered the tank to recover the data-logger by pulling on the release tab of the elastic strap. Upon retrieval of the device, the data-loggers were downloaded to a laptop using software provided by the accelerometer manufacturer. Stopwatch time was then converted to data-logger time using the video of the data-logger synchronisation event to calculate and add an offset to each timestamp using R (version 2.15.2; R Development Core Team, 2012). The segment of running stopwatch video that preceded each deployment also was used to convert video frames to stopwatch time, and from stopwatch time to logger time, bringing everything onto a common time series.

The static component of acceleration, the component due to gravity, was removed from the acceleration signal by smoothing the record with a running mean of three seconds using the Box smoothing algorithm in IGOR Pro across 15 data points, with End Effects set to 0, then subtracting this result from the raw signal to leave only dynamic

acceleration (Figure 3). It is suggested that the running mean selected for smoothing be greater than one stroke cycle of the focal animal (Shepard et al., 2008). Shepard et al. (2008) found that a running mean of 3 s provided a robust minimum for species with a stroke length <3 s. Preliminary observations revealed a stroke cycle between one and two seconds for specimens of common smoothhound.

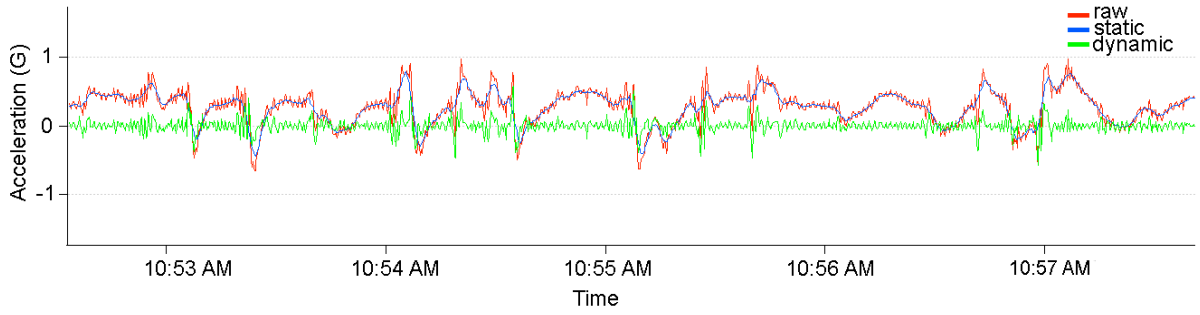

Figure 3. Example of the derivation of static and dynamic acceleration from the raw acceleration trace (red) in a typical shark. The blue trace represents the static time series estimated by a 3 s running mean, and green the dynamic time series calculated by subtracting the static from raw acceleration.

The ability of the analysis to discriminate different swimming behaviours relies on the assumption that the accelerometer can accurately measure individual tail beats (Chapter 1). This relationship was tested for my study specimens by measuring TBF across several 5 s observation windows from video footage. Observation windows were randomly generated with a target of one observation window for every minute of video. TBF was then calculated from the video footage for each observation window by counting the number of complete stroke cycles observed divided by the duration of the observation window. Observation windows where the shark was not in view or was not undergoing clear bouts of steady swimming were discarded. TBF was then also calculated autonomously from the accelerometer record by measuring the dominant frequency of a Power Spectrum Density (PSD) analysis, using the dominant.freqs function of the GeneCycle package for R (Ahdesmäki et al., 2007). The pooled TBF estimations from video and from accelerometer were then compared with a paired Wilcoxon signed-rank test.

The ability of the accelerometer to detect body attitude from the gravitational component of acceleration was also tested. The arcsine of the static acceleration in the surge axis was calculated and averaged for each second of the deployment (Equation 1; Figure 4), where γ_i is the body angle, A_i the acceleration in the surge axis, G the

acceleration of gravity (1 G), and $\Delta\gamma$ the attachment angle of the accelerometer (Sato et al., 2003).

$$\gamma_i = \sin^{-1}\frac{A_i}{G} - \Delta\gamma \quad (1)$$

Body angles were converted to categories of "Incline," "Neutral," and "Decline" using the same definitions used for visual observation. These annotations were then compared against the observed swimming postures by calculating true and false detection rates. True detection rate was taken as the number of postural states identified by both the accelerometer method and the visual observation, divided by the number of postural states observed only by the visual method. False detection rate was taken as the number of postural states identified only in the accelerometer record, divided by the total number of postural states identified by the accelerometer method.

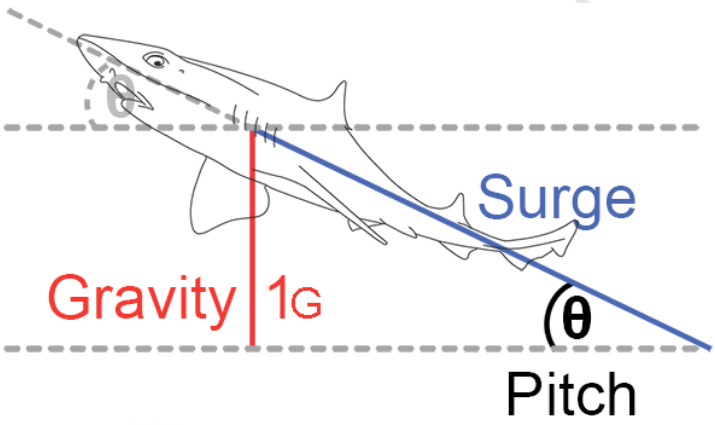

Figure 4. Illustration demonstrating the trigonometric derivation of body angle from the acceleration recorded in the surge axis and the constant 1 G of the gravitational field on Earth.

Data recorded by the accelerometers were then categorised into behavioural categories using several methods based on the frequency and amplitude of tail beats. Body angle was also estimated as the arcsine of the static acceleration in the surging axis (Sato et al., 2003).

The first method of behavioural categorisation relied on manual inspection of the dynamic sway acceleration record as in Gleiss, Gruber, & Wilson (2009), annotating the accelerometer record into per-second states of steady swimming, gliding, resting, or bust swimming based on visual approximations of tail beat frequency and amplitude. The accelerometer record was then categorised autonomously per-second by employing the k-means clustering function to a continuous wavelet transformation of

the data using an algorithm available in Ethographer. The continuous wavelet transformation was generated using a minimum cycle duration of 0.4 s, a maximum cycle duration of 5 s, and a mother wavelet parameter of 16. These cycle values highlighted the area of possible stroke durations and produced a mother wavelet with a fair balance of resolution in time and periodicity. The software was programmed to oversample the data into 10 clusters in an attempt to increase the ability of the method to differentiate between transitional swimming patterns like the shift from swimming to gliding. Similar spectra were then regrouped into 2-4 clusters to represent the different behavioural states (Figure 5) as these elements may represent the same behavioural pattern, differing only in intensity or periodicity (Sakamoto et al., 2009). For each method, analysis time, and true and false detection rates were compared for behaviours when analysed with visual observations on a second-by-second basis. Detection rates were calculated for each behaviour class in a manner identical to the calculation for postures.

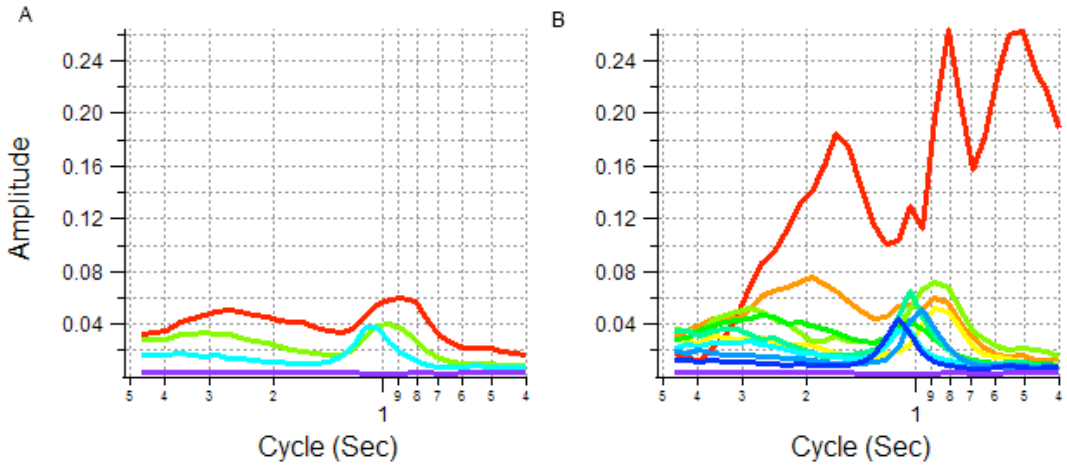

Figure 5. Example spectrum criteria generated by the k-means clustering algorithm in Ethographer. (A) Shows criteria generated when four clusters are chosen. (B) Shows criteria generated when 10 clusters are chosen. Note in (A) that the low frequency trace (green) characteristic of gliding displays a high degree of similarity to the trace representative of steady swimming (blue). In (B) the gliding spectrum (orange) is more distinct. In this case I combined the blue, green, and yellow clusters representative of steady swimming, retaining red for burst swimming, orange for gliding, and purple for resting.

RESULTS

A total of 28 hours of accelerometer data were recorded from five sharks for a total of 503953 data points (Table 1). TBF was estimated by calculating tail beats across 646 5-s observation windows of video footage and comparing this value to an estimate derived from the accelerometer record. The distribution of values calculated by these two

methods shared many similar characteristics (Figure 6), but a histogram of the methods revealed a departure from normality (Figure 7), consequently a non-parametric test was used to assess their differences.

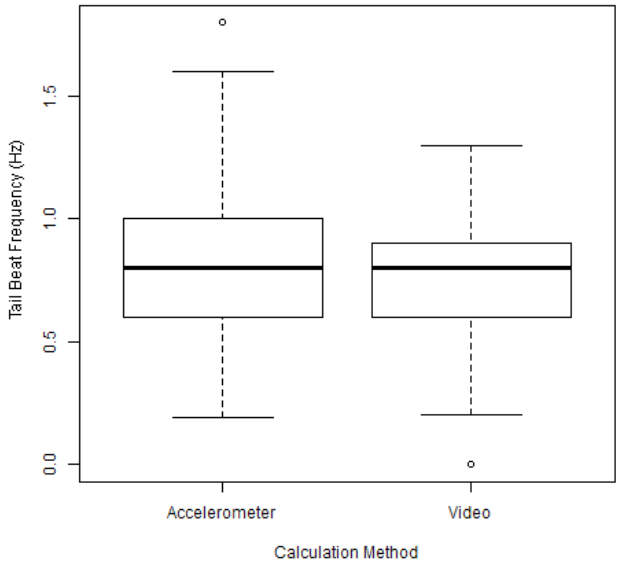

Figure 6. Box and Whisker plot of the distribution of Tail Beat Frequencies calculated by measuring the dominant frequency in a Power Spectral Density analysis of the accelerometer record across random 5-second windows of accelerometer records and video footage

There was no difference between TBF estimated by the accelerometers (0.76 ± 0.29 Hz; mean ± SD) and video observations (0.77 ± 0.19 Hz; Wilcoxon signed-rank test V = 61436.5, p = 0.3286). However, a post-hoc computation of statistical power using G*Power 3.1.5 (Faul et al., 2007) revealed a theoretical minimum power of only 0.15.

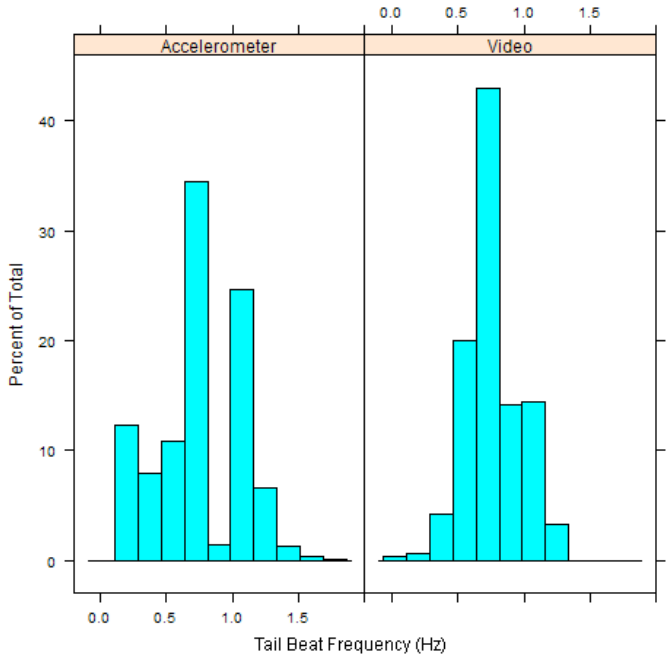

Figure 7. A Histogram of Tail Beat Frequencies grouped by observation method, showing departures from normality, especially for the accelerometer data.

The arcsine of the accelerations in the surge axis were calculated for each data point to generate an estimate of device angle for each second. A mean device offset angle was calculated from periods when the sharks were observed resting on the tank bed and subtracted from the device angle to derive body angle. Comparing these calculations of body angle to estimates from visual observations resulted in a successful identification rate for inclined swimming of only 22.8 ± 14.5% (mean ± S.D.; 89.5 ±7.6% false detection rate). Neutral swimming, between the angles of +45° and -45°, was correctly inferred 77.2 ± 11.0% of the time (8.2 ± 6.4% false detection rate). Swimming in a declined posture was detected correctly only 47.6 ±25.3% of the time, with 79.8 ±17.0% of detections being false positives

Tail beat frequency and amplitude inferred from dynamic acceleration in the sway axis were used to categorise behaviours by manual interpretation and by autonomous interpretation with the Ethographer computer software, and were compared for accuracy with visual observations of the instrumented sharks (Figure 8).

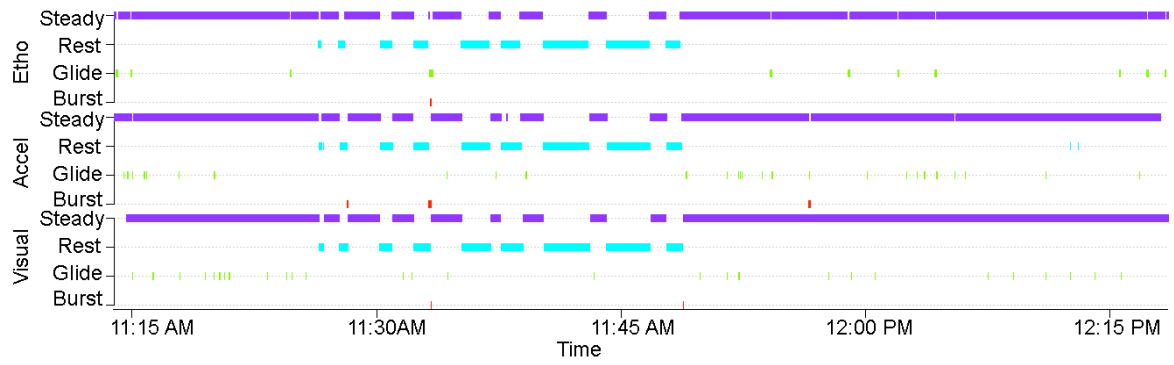

Figure 8. Comparison of observed behavioural states for one deployment. The method of classification is identified on the left axis. Each coloured bar represents one of four behavioural states. The accuracies of each experimental method (Accel, Etho) were compared against the visual record of the deployment.

The accelerometer record from each deployment was categorised into behavioural states by visually approximating frequency and amplitude from a line graph of the time series (Figure 9).

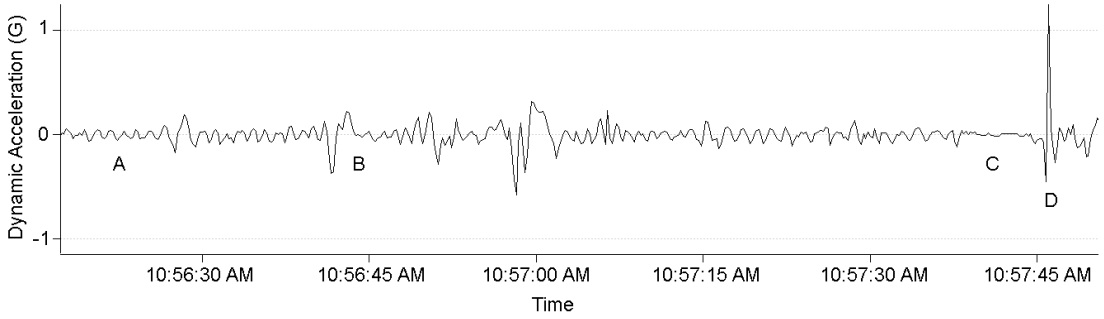

Figure 9. Example accelerometer trace showing a subset of the dynamic acceleration in the sway axis for one deployment. (A) shows a portion of the trace thought to be indicative of steady swimming, (B) Gliding, (C) Resting, and (D) Burst swimming.

Peaks in the sway axis of the dynamic acceleration record were interpreted as tail beats with each positive and negative peak corresponding to one complete stroke cycle as revealed by the TBF analysis and in Tanaka, Takagi, & Naito (2001). Bouts of constant amplitude and frequency identified visually in the record were interpreted as characteristic of steady swimming (Figure 9). A detection rate of 97.4% and a false detection rate of 1.8% were achieved for the steady swimming behavioural state (Table 2). High frequency and high amplitude peaks in the accelerometer record where acceleration in the sway axis measured above 1 G were interpreted as resulting from sudden, sharp tail beats observed in fast start swimming (Figure 9). However, I only detected burst swimming successfully 19.4% of the time with these criteria (85.6% false detection rate; Table 2). Gliding states were inferred from the accelerometer record when sway acceleration showed a sudden decrease to 0 G followed by a period of very

small oscillations at or around 0 G (Figure 9). This was taken to indicate slow movement without any pronounced tail propulsion, but the detection rate was only 9.3% (false detection rate 94.9%; Table 2). Resting behaviour was defined as an absence of any tail beats combined with the absence of movement altogether. Periods in the accelerometer record when the sway axis recorded a constant 0 G were inferred to correspond to periods where the shark lay motionless on the tank floor (Figure 9). This method achieved a 63.3% detection rate, coupled with a 55.2% false detection rate (Table 2).

Table 2. Mean (± S.D.) detection rates for different behaviours using the two analysis methods. True detection rates calculated as the percentage of visually observed behavioural states also detected experimentally. False detection rates calculated as the percentage of experimentally detected behavioural states that were not observed visually.

Method	Manual		Ethographer	
Behaviour	True (%)	False (%)	True (%)	False (%)
Steady	97.4 ± 1.8	1.6 ± 1.4	92.5 ± 6.4	2.1 ± 2.1
Burst	19.4 ± 19.8	85.6 ± 15.0	33.7 ± 32.4	87.4 ± 13.9
Glide	9.3 ± 9.3	94.9 ± 6.4	4.7 ± 6.4	94.4 ± 20.7
Rest	63.3 ± 40.9	55.2 ± 43.0	36.0 ± 45.0	58.7 ± 44.2

Following the manual annotation, an autonomous approach was then investigated. Ethographer was used to approximate the dynamic acceleration with a continuous wavelet transformation. The resulting spectrogram (Figure 10) was then analysed with a k-means clustering analysis (Figure 5) to identify the specific behavioural states. Using this approach, I could analyse an average of 1616.9 ± 139.7 data points.s^{-1} (mean ± S.D.), compared with an average of 11.7 ± 5.4 data points.s^{-1} when the accelerometer record was annotated visually.

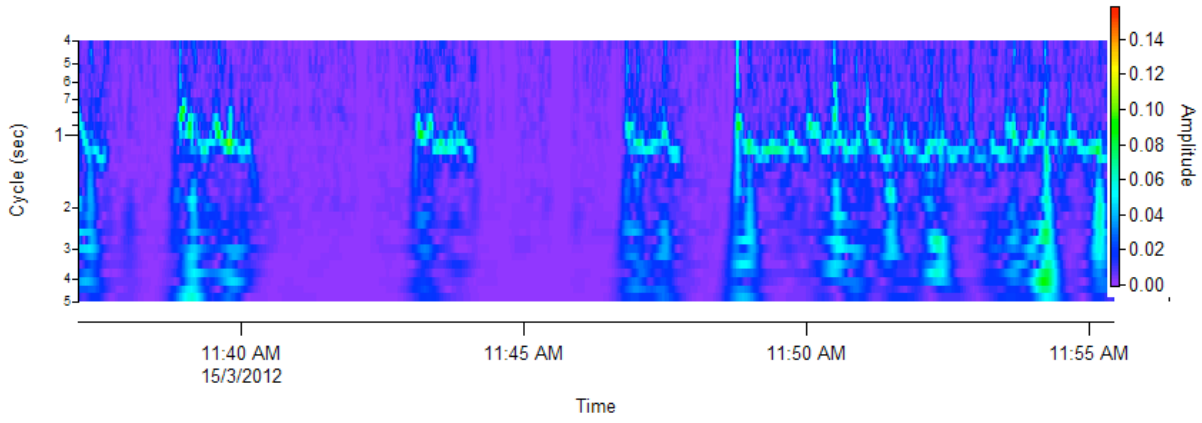

Figure 10. Example spectrogram generated by a continuous wavelet transformation of the dynamic acceleration record in the sway axis for one deployment. The left axis identifies the stroke cycle duration of the tail beats, and the coloured axis represents the amplitude.

Clusters identified with a peak amplitude corresponding to a cycle duration in the range of our observed mean tail beat frequency were taken to be indicative of steady swimming (Figure 5). Using these criteria, a detection rate of 92.5% and a false detection rate of 2.1% were achieved (Table 2). Clusters defined by their high frequency and high amplitude were interpreted as indicative of burst swimming states (Figure 5). With this approach, burst swimming was identified with a 33.7% detection rate and 87.4% false detection rate (Table 2); still poor, but better than manual coding. Gliding was inferred from clusters with a strong low frequency component (Figure 5), but this only gave a detection rate of 4.7% and a false detection rate of 94.4% (Table 2). Resting was characterised by the absence of discernible peaks in stroke cycle. Ethographer identified resting behaviour with a 36.0% detection rate and 58.7% false detection rate (Table 2).

In the three deployments where behavioural and postural observations were recorded *post hoc* from video by the author as opposed to *in situ* during experimentation from multiple observers, I found improvements in the true detection rates for burst, gliding, and resting. Detection rates of 68.8 ± 44.2%, 10.4 ± 9.4%, and 55.9 ± 48.7% (mean ± S.D.) were achieved in the Ethographer analysis of these deployments, compared with the 33.7%, 4.7%, and 36.0% detection rates achieved in the entire study (Table 2). False detection rates for these behavioural types, and true and false detection rates for steady swimming remained similar to values for the whole study sample.

The relationship of Overall Dynamic Body Acceleration (ODBA) to TBF (Hz) and TL was modelled for all sharks (Figure 11). ODBA was calculated as the sum of the absolute value of the accelerations in each axis as in Wilson, et al. (2006). A significant relationship between ODBA and the predictor variables was found according to ODBA = 0.0715*TBF - 0.0005*TL + 0.1687. All p values were less than 0.05 and the model showed an R^2 value of 0.03. A positive relationship between TBF and ODBA is similar to the relationship found for other shark species (Gleiss, Gruber, & Wilson, 2009).

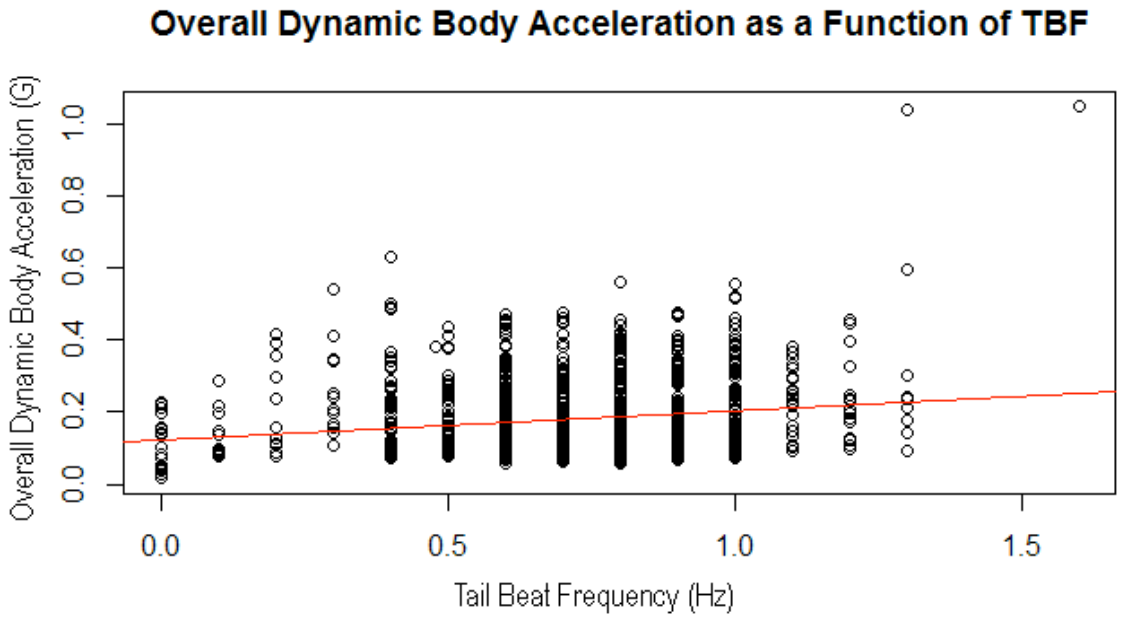

Figure 11. Relationship between ODBA and TBF for all sharks. A linear regression was fit to the data (red). For display purposes, only the coefficient relating the TBF is included in the plot of the regression.

Using this relationship of TBF to energy expenditure, theoretical estimations of OBDA were calculated for a number of control experiments and compared with empirical estimations of ODBA calculated during experimental deployments (Figure 12). For two of the sharks used in this experiment, unstressed TBF was calculated from video recordings in the same manner used for the TBF analysis by monitoring the sharks swimming in the tank prior to attachment of the data-logger. Stressed TBF was calculated in the same manner after having put the shark through the tagging motions by capturing the individual, attaching the data-logger, and then removing the data-logger before allowing the shark to swim throughout the tank.

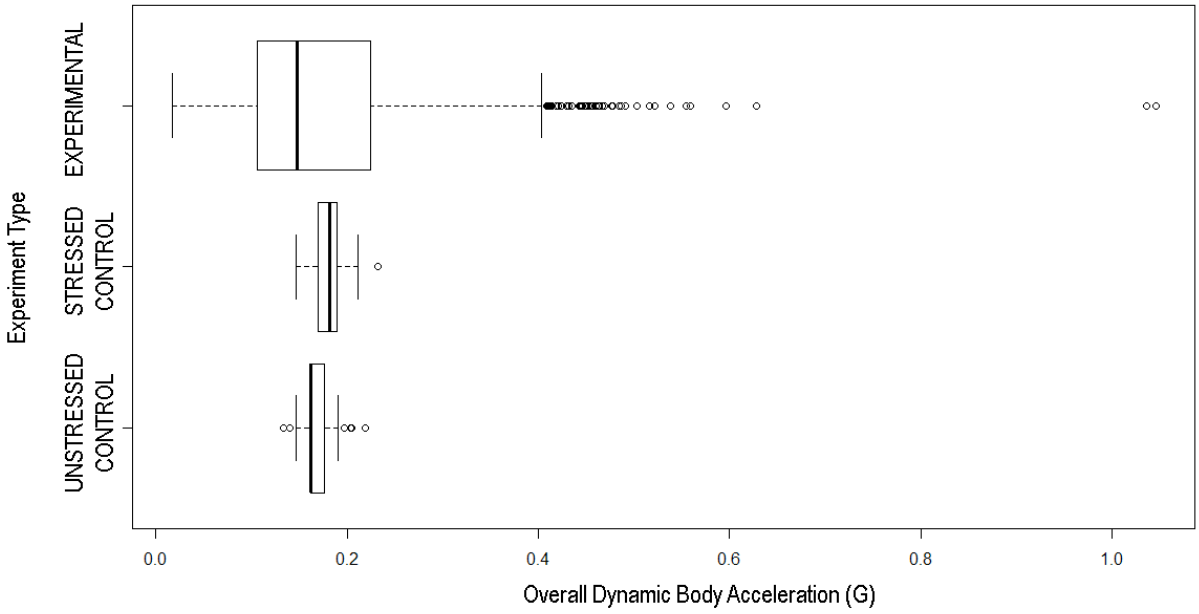

Figure 12. Estimates of Overall Dynamic Body Acceleration for sharks with and without accelerometers with two stress levels among the control group. There are significant differences among all three groups (see text for details).

ODBA was then estimated for untagged control sharks by inputting the observed TBF and TL into the model generated above. Mean ODBA estimated for sharks swimming in the unstressed control condition using the TBF model was 0.167 ± 0.012 (mean ± S.D.). Mean ODBA estimated similarly for sharks swimming in the stressed control condition without data-loggers was 0.179 ± 0.014. Lastly, ODBA calculated for sharks swimming with data-loggers directly from the accelerometer was 0.181 ± 0.107. A Kruskal-Wallis rank sum test was performed on the ODBA values for each experiment type using the kruskal.test() function in R resulting in a X^2 value of 45.239 (df=2, p<0.001). The result of this test rejects the null hypothesis that ODBA is the same across all three groups. A *post hoc* Wilcox rank test also revealed significant differences among each test group (stressed/unstressed; W=28254, p <0.001, unstressed/exp; W= 200041.5, p <0.001, stressed/exp; W=112771, p<0.001) confirming the results of the Kruskal-Wallis test.

DISCUSSION

My findings do not help to confirm the ability of tri-axial accelerometers to detect the fine-scale movements of sharks, unlike other similar studies that indicate an important role for the device in the larger movement ecology paradigm (Whitney et al., 2012). The tail beat frequency calculated from the accelerometer data was the same as that

determined from video observations, and was similar in frequency to that reported for sharks of comparable size (Gleiss, Gruber, & Wilson, 2009). This principle establishes the basis for the accelerometry technique as further analyses are based on the supposition that the accelerometer can accurately detect the frequency and amplitude of tail or fin movements (Shepard et al., 2008). Beyond this relationship, however, this study largely fails to demonstrate the utility of accelerometers for studies of *Mustelus mustelus* movement.

The ability of the accelerometer to detect individual tail beat movements is sensitive to a number of assumptions. The first point of importance is the selection of a suitably high sampling rate, such that all phases of the stroke cycle are measured accurately (Shepard et al., 2010). The sampling frequency should be at least twice the animal's Nyquist frequency, that is twice the rate of the highest expected frequency of movement, or frequent enough to record 10 samples per tail beat (Whitney et al., 2012). This is scale dependent, so the sampling frequency necessary to measure the tail beat frequency of a large whale shark, 4 Hz, is inappropriate for measuring the tail beat frequency of a much smaller bonnethead shark (*Sphyrna lewini*), 20 Hz (Gleiss et al., 2010; Gleiss, Norman, & Wilson, 2011). In this study, sampling rate was limited by the small memory capacity of the data-logger, however the 5 Hz sampling rate appeared sufficient to measure the 0.76 ± 0.29 Hz tail beat frequency of captive smoothhound sharks.

The second point of concern when measuring tail beat frequency via accelerometry is the sensitivity of the data-logger to position on the animal. Traditionally, the dorsal fin has been selected for tag attachment in sharks (Hammerschlag et al., 2011), but this site is not suited for accelerometry studies due to the flexible nature of the dorsal fin and the necessity for a noise-free environment when recording acceleration (Lingham-Soliar, 2005). Previous researchers have recommended a direct body attachment near the caudal peduncle for measurement of tail beat frequency (Whitney et al., 2007; Gleiss, Gruber, & Wilson, 2009). According to Newton's third law of motion, all forces exist in pairs; for every action there is an equal and opposite reaction. This is apparent in the lateral repetitive motion of a fish tail during locomotion; during a power stroke, the lateral motion of the tail in one direction produces a simultaneous and opposite movement in the trunk (Shepard et al., 2010). It is thus appropriate to position the tag close the centre of mass as this will record the reactionary force of movement from any

part of the body (Gleiss, Wilson, & Shepard, 2011). The magnitude of the reactionary force measured depends on the position of the tag along the body, so tag position must be held constant if values are to be compared among or within species (Shepard et al., 2010).

My tag placement along the ventral surface of the shark, anterior to the pelvic fin resulted in accurate measurement of undulating locomotion; however in one individual the elastic strap produced a swelling and discolouration under the strap. It is thus important to further investigate the impact of tagging on instrumented individuals. In addition to the physiological stress of capture, there is a risk of habituation to repeated capture. A change in the composition of the behaviours performed by each shark was noted as individuals were subjected to successive deployments, peaking at deployment two for most sharks (Figure 13). During deployment two, there is a sharp decrease in steady swimming, and a concurrent increase gliding, resting behaviours. Burst swimming shows a later peak around deployment number four. Following these deployments there is an increase in the time spent steady swimming, and decreases in the time engaged in other behaviours. Initial high rates of burst swimming and resting might result from attempts to shed the tag or to recover from the tagging process. As each shark was increasingly exposed to capture, the prevalence of these behaviours diminished, perhaps representative of an initial alteration of behaviour before returning to more natural levels. Surgical implantation might be considered if devices can be deployed for longer durations. This also would obviate any drag-associated impact caused by the logger, and coupled with a larger memory capacity, remove the need to repeatedly recapture the animal.

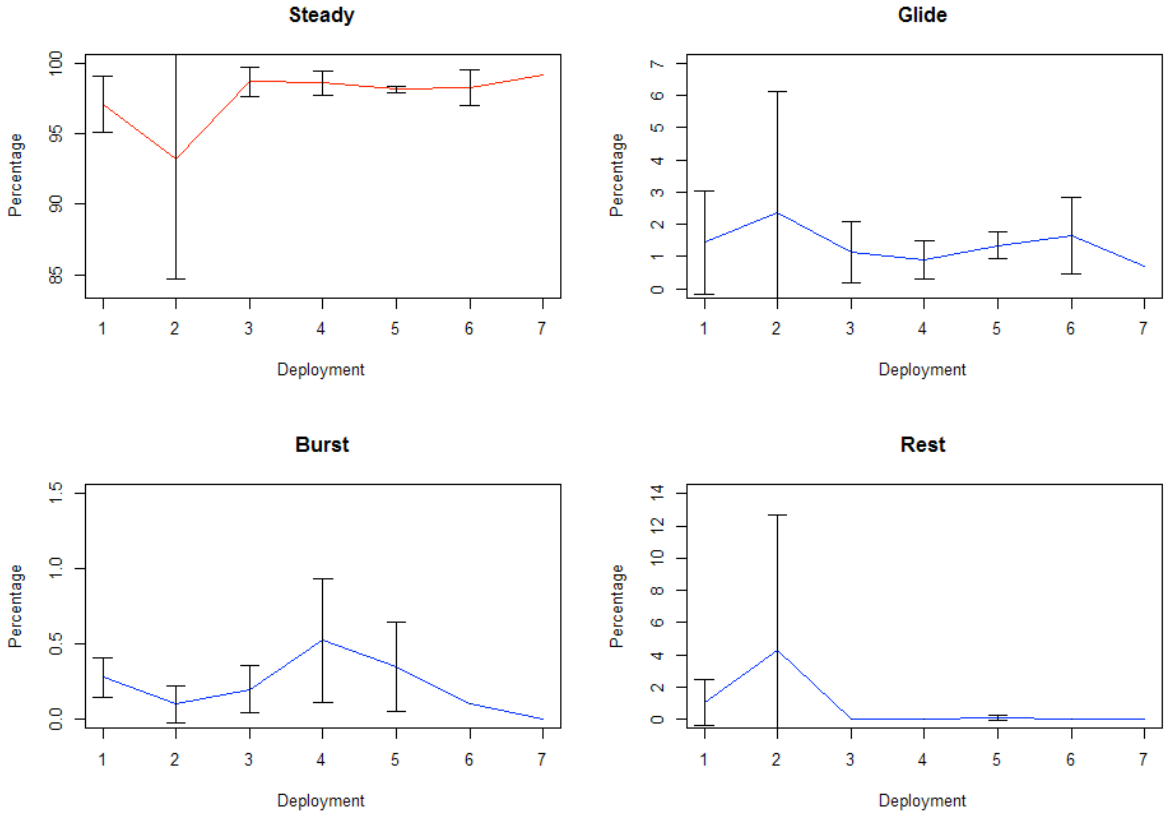

Figure 13. The changing composition of behaviour as individuals underwent successive deployments. Mean ± S.D.% is given for each deployment (n=5 individuals).

The approach used to infer body angle largely failed, despite the use of coarse thresholds to define posture. The inadequacies of this method may be due to several limitations of the methodology, the first of which is the coarse calibration of device angle. It is very difficult to align the logger parallel with the longitudinal axis of the animal, and as a result some offset will be necessary to derive the true body angle from the angle of the data-logger. Previous studies have calibrated logger orientation by noting when fish were resting horizontally, but this may not be practical for obligate-ram ventilators (Kawabe et al., 2004). Not all deployments in this experiment included bouts of resting on the surface of the substrate, so an overall calibration angle was calculated for those sharks that did, and used for all sharks, which may account for some of the discrepancy in our record. Kawatsu et al. (2010) present a novel method for *post-hoc* determination of logger angle when a speed sensor is included in the logger.

An offset in logger angle may account for some of our high false detection rates when body angle was near threshold values for the different postures, but the sensitivity with which the accelerometer measures pitch may also be a contributing factor. Pitch is

derived from the arcsine function of acceleration in the surge axis. Due to the changing function of the arcsine of the surge axis, the range of body angles that provides the most sensitivity falls within the zone considered neutral swimming. This bias in sensitivity may thus account for the high degree of accuracy and low false detections within the neutral range, and the lower accuracy and higher rate of false detections for swimming classified as inclined and declined.

The calculation of swimming angle is based on the static component of the acceleration record, which is approximated from the raw acceleration record by estimating the low frequency oscillations with a running mean or band-pass filter. The length of the running mean or the parameters of the band-pass filter are dependent upon the stroke cycle of the animal. For a running mean approach, the smoothing window is selected such that it is long enough to exclude dynamic movement, by being at least greater than the length of one stroke cycle, but short enough to detect erratic movement patterns. For the analogous filter approach, the band-pass filter is designed so that the low-pass cut-off is lower than the stroke cycle frequency, allowing only low frequency oscillations associated with gravitational acceleration to pass. Shepard et al. (2008) suggest a running mean of 3 s for species with a stroke cycle up to that value, but also offer a method for calculating the appropriate value. The 3 s running mean used in this experiment may have been too large for the 0.76 ± 0.29 Hz stroke cycle, resulting in some elements of the static component being erroneously smoothed out of the signal and attributed to the dynamic component. Calculation of a more suitable running mean or the tuning of a band-pass filter may help to improve the detection rates achieved in this study.

Above all else, the most likely source of the high deviations within detections rates for this study was in the use of multiple observers for the recording of behavioural and postural observations. While each behavioural and postural state was defined prior to experimentation and kept constant throughout the duration of the study, the observers were only briefly trained prior to their individual surveys. The nature of the program supplying volunteers limited the available time for training exercises. In previous studies, researchers were able to effectively minimise bias among and between observers in previous studies by careful training and calibration and should be considered for future experimentation (Thompson & Mapstone, 1997).

The choice to record observations from live observation may also have introduced a degree of false detection due to the reaction time between making an observation, checking the stopwatch, and recording the observation. While the observational record was preserved in video form during this study, it was not used to annotate behaviour and posture for all deployments. Future studies would benefit from preserving the observational record to make annotations at a later time. A possible remedy for this discrepancy might be to include a search window in the calculation of detection rates such that behaviours would be considered identical if they were detected between methods with a time difference of less than or equal to 3 s (Okuyama et al., 2009). Another possible solution to increase the detection rates and decrease the false detection rates might be to include accelerations from other axes in the analysis, as only accelerations in the sway axis were used to perform the categorisation in this study. Incorporating changes in posture, for instance, may help improve the detections of gliding behaviour, as this can be deduced from the declined swimming posture of the animal. The impact of the multi-observer bias and reaction time bias were also present in the behavioural categorisation analysis due to the similar methodology.

An incomplete visual record as a result of observer bias may introduce false detections, but more important, is the assumption that the visual record represents the true record. While convenient for the calculation of detection rates, this assumption is not valid as the objective techniques used by Ethographer have the ability to identify changes in behavioural spectra that may be too subtle to observe with the naked eye. This is demonstrated by the clustering of steady swimming into multiple similar spectra, differing only in the intensity and periodicity of tail beats (Figure 5; Sakamoto et al., 2009).

In spite of high rates of false detection for both the postural and behavioural analysis, there was still some degree of biological relevance. Most notable, is the ability of the logger to differentiate between periods of activity (steady swimming) and inactivity (resting) with a high detection rate, reflecting results found in earlier accelerometer deployments (Whitney et al., 2007; Gleiss, Gruber, & Wilson, 2009). This represents an important change in behaviour that can be difficult to detect by common tools such as acoustic and satellite telemetry without suitable coverage (Naesje et al., 2012; Whitney et al., 2012; Postlethwaite & Dennis, 2013; Thiebault & Tremblay, 2013). Detecting

periods of activity and inactivity in the field can reveal diel movement patterns, resting areas, and give further insights into the energetic budget of sharks.

Despite the limited success in detecting behaviour and a lesser ability to accurately detect posture, autonomous analytical approaches like that found in Ethographer are recommended for investigating movement ecology with accelerometers. Numerical techniques such as these provide the necessary computational power to process large datasets and also provide objectively quantitative methods for measuring fine-scale movement. The ability to process nearly 140 times the data in the same time with the same degree of accuracy as visual methods is sufficient reason to further develop these techniques.

The true contribution to the field of movement ecology however, will come from the ability of the accelerometer to measure activity specific energy expenditure. In the aquatic environment, animals experience a continual loss of energy to the external medium in the form of swimming drag. In terrestrial animals this loss occurs though ground deformation. The replenishment of this energy is manifested in the form of mechanical work; the movement of the animal though its environment. Movement is a product of the motion of limbs, requiring muscular contraction and the hydrolysis of ATP, the energetic currency of biology. Thus by measuring movement, we are effectively measuring the expenditure of energy (Gleiss, Wilson, & Shepard, 2011). Considerable progress has been achieved in using the analytical technique of Overall Dynamic Body Acceleration (ODBA) as a proxy for energy expenditure. This *in situ* approximation of energy expenditure has the potential to reveal much about the motivation for movement and will help further our understanding of the linkages between different scales and components of the movement ecology paradigm.

In this experiment, ODBA was used as an indicator of activity level and thus as an indication of the animals stress due to handling and carrying the data-logger. This experiment allowed me to assess the stress associated with capture and handling, and the stress associated with carrying the logger. Capturing the shark introduced a degree of stress, as did the act of carrying the logger. Utilising an anaesthetic during tag attachment and allowing the animal sufficient time to recover from the tagging process would benefit future studies. In this experiment, a recovery period was not possible due

to the small memory capacity of the logger, but modern technological advances are producing loggers with much larger data-storage capabilities and delayed start technologies that would allow for a recovery period before experimentation. These results reflect the need for further miniaturisation and attachment techniques mentioned previously (Bannasch, Wilson, & Culik, 1994), but also provide the foundation for utilising ODBA as a measure of an animal's stress response, such as that found after capture-and-release (Skomal & Chase, 2002; Marshall et al., 2012).

CHAPTER 3. SYNTHESIS, CONCLUSIONS, AND FUTURE DIRECTIONS

The results of this study show the foundations of some promise for the use of accelerometers in the description of shark swimming behaviour; however the methods for assessing this power and the techniques used to analyse the data are still relatively new technologies in need of much further calibration and development. There is a current trend toward analysis techniques involving machine-learning algorithms for statistical pattern recognition, such as Support Vector Machines and Hidden Markov Models (Mannini & Sabatini, 2010; Nathan et al., 2012; Gao et al., 2013). Though similar to the k-means clustering algorithm, these techniques differ in that they are first trained on sample datasets. Early assessments of machine learning methods are proving to be successful for autonomous pattern recognition, resulting in detection rates as high as 83–94% in some studies (Grünewälder et al., 2012).

The obvious next step for future experimentation would be to see deployment on free-swimming individuals. It was my original intention to place the tag on the dorsal region, such that the methodology could be scaled up for larger sharks, however the fin attachment method proved unsuccessful in preliminary testing. The principles of accelerometry necessitate fixed placement along the body of the animal, however for larger sharks this can be problematic as it is often difficult to remove them from the water. The flexible nature of the dorsal fin has the potential to introduce noise into the accelerometer reading (Lingham-Soliar, 2005; Gleiss et al., 2009), but has been successfully utilised as an accelerometer attachment site for the detection of mating behaviours in nurse sharks (Whitney et al., 2010). To avoid snagging and slipping of the data-logger it is suggested that accelerometers be hydrodynamically attached through the dorsal fin. Nakamura et al. (2011) presented a novel design for an accelerometer tag package that included a VHF tag and accelerometer that was programmed with a time-release mechanism to burn the attachment to the dorsal fin and float to the surface for recovery. The logger was cable-tied through the dorsal fin to prevent slipping, and was hydrodynamically shaped such that no hard edges that could snag elements of the marine environment protruded from the dorsal fin. In order to recover the data-loggers, these free-swimming deployments would need to be coupled with GPS loggers. This

would also provide researchers with the necessary information to associate specific swimming patterns and behaviours with specific areas and evaluate the energy expenditure along each pathway in a quantitative manner (Nathan et al., 2012).

An alternative to GPS coupling for data-logger recovery are accelerometers that transmit a summary of their sensor data to an acoustic receiver, such as those manufactured by Vemco® (Murchie et al., 2011; Payne et al., 2011). These data-loggers transmit a vector sum or root-mean-square of acceleration in all three axes over time. This value is similar to ODBA and represents an overall acceleration value for the tagged animal. The long battery life and the ability to transmit data acoustically provide considerable benefits for free-swimming deployments when compared to the data-logger used in this study; however the inability to transmit a full record of acceleration generally limits their use to studies for metabolic rate and energy expenditure rather than description of behaviour.

A potential source of noise during free-swimming deployments will be the surging wave action that can sometimes tumble smaller species like the smoothhound. Researchers have successfully detected resting within the surge zone in sharks using Ethographer, however it is not known if this method will be applicable to smaller sharks like the study species in this study (Whitney et al., 2010). This also begs the question of allometry with regards to the accelerometry technique. Researchers using accelerometers to investigate the evolution of locomotory patterns found a high degree of similarity between different species of differing size (Gleiss et al., 2011), suggesting that the behavioural analysis technique might apply to a range of scales. Studies of the relationship of body acceleration to oxygen consumption however, have shown that while being an excellent predictor of oxygen consumption, the relationship between ODBA and energy expenditure shows some variation between species and to a lesser degree, within some species (Halsey et al., 2009). The physics of undulating motion remain similar across differing scales, with only the power of such motion changing with body mass. This would suggest that the technique for behavioural and postural analysis would remain effective for animals of similar locomotory patterns, but the technique for estimating energy expenditure would require an individual calibration.

The *in situ* measurement of energy expenditure has the potential to impact best practices in the same way that the identification of location specific behaviours might help improve conservation strategies. Catch-and-release has become a popular approach to sport fishing for the conservation-minded angler. A number of studies have investigated the physiological effects of capture on the blood chemistry sharks (Skomal & Chase, 2002; Marshall et al., 2012). The accelerometry technique provides a less invasive method for the quantification of the post-capture stress response, allowing the quantification of locomotory patterns and energy expenditure after capture. The post-capture response of the sharks used in this experiment are analysed as a demonstration of this approach.

Table 3. Bayesian Information Criterion values for models of ODBA incorporating various fixed and random effects. Random effects are identified by parentheses.

Model Description	BIC
Capture.Time+(1|Deployment ID)	-4471.763
Capture.Time+Time+TL+(1|Deployment ID)	-4439.267
Capture.Time+Time+TL+(1|Shark ID)+(1|Deployment ID)	-4437.327
Capture.Time+Time+TL+(1|Shark ID)	-4029.776
Capture.Time+Time+TL	-3779.235
Capture.Time+Time+TL+Weight	-3774.163

The methodology employed in this study required the repeated capturing and handling of the shark prior to each deployment. Capture and handling time was recorded for each deployment as an indication of stress level. This information was used along with a calculation of ODBA to model the stress response of the sharks. A linear mixed effects regression was fit to model the relationship of Capture Time (CT, min), Total Length (TL, cm), and Time After Catch (TAC, min) to ODBA using the lmer() and lm() function of the R package lme4, and using the Bayesian Information Criterion (BIC) to select the best-fitting model (Table 3; Schwarz, 1978). The relationship between the response and the terms was defined by ODBA = -0.0005*TAC + 0.2241, with a random intercept term included for Deployment ID to account for non-independence of data. The negative slope of the TAC coefficient suggests that the energy expenditure of the shark shows a negative relationship with time after catch, indicative of a response to the stress event. Studies expanding on this design might help to determine best practices for anglers to maximise post-capture survival such as optimal fight and handling times.

Lastly, as an effort to encourage the process of scientific development and allow for the wide-range replication of experimental conditions, it is recommended that future analyses utilise the open-source and free R Project for Statistical Computing. While Ethographer and IGOR Pro were used for its convenient accelerometer-specific analysis tools, R also has packages that support the continuous wavelet transform and k-means clustering algorithms. The constant development of this software and its packages make it an attractive tool for future analyses.

REFERENCES

Ahdesmäki, M., Lähdesmäki, H., Gracey, A., Shmulevich, I., & Yli-Harja O. (2007). Robust regression for periodicity detection in non-uniformly sampled time-course gene expression data. *BMC Bioinformatics, 8*, 233.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*, 227-267.

Altmann, S. A., & Altmann, J. (2003). The transformation of behaviour field studies. *Animal Behaviour, 65*, 413-423.

Arai, H. (1997). Collecting, transporting and rearing of the scalloped hammerhead. *Proceedings of the Fourth International Aquarium Congress,* Tokyo, Japan. 87-89.

Arai, N., Kuroki, M., Sakamoto, W., & Naito, Y. (2000). Analysis of diving behavior of Adélie penguins using acceleration data logger. *Polar Bioscience, 13*, 95-100.

Au, D., & Weihs, D. (1980). At high speeds dolphins save energy by leaping. *Nature, 284*, 548-550.

Baldridge Jr., H. D. (1972). Accumulation and function of liver oil in Florida sharks. *Copeia, 1972*, 306-325.

Bannasch, R., Wilson, R. P., & Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *The Journal of Experimental Biology, 194,* 83-96.

Block, B. A., Costa, D. P., Boehlert, G. W., & Kochevar, R. E. (2002). Revealing pelagic habitat use: The tagging of Pacific pelagics program. *Oceanologica Acta, 25*, 255-266.

Block, B. A. (2005). Physiological ecology in the 21st century: Advancements in biologging science. *Integrative and Comparative Biology, 45*, 305-320.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A.-L., Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R., Shillinger, G. L., Schaefer, K. M., Benson, S. R.,

Weise, M. J., Henry, R. W., & Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature, 475*, 86-90.

Boehlert, G. W., Costa, D. P., Crocker, D. E., Green, P., O'Brien, T., Levitus, S., Le Boeuf, B. J. (2001). Autonomous pinniped environmental samplers: Using instrumented animals as oceanographic data collectors. *Journal of Atmospheric & Oceanic Technology, 18*, 1882-1893.

Bonfil, R., Meÿer, M., Scholl, M. C., Johnson, R. L., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D., Paterson, M. (2005). Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science, 310*, 100-103.

Bouten, C. V., Westerterp, K. R., Verduin, M., & Janssen, J. D. (1994). Assessment of energy expenditure for physical activity using a triaxial accelerometer. *Medicine and Science in Sports and Exercise, 26*, 1516-1523.

Boyd, I. L., Kato, A., & Ropert-Coudert, Y. (2004). Bio-logging science: Sensing beyond the boundaries. *Memoirs of National Institute of Polar Research, Special Issue, 58*, 1-14.

Bres, M. (1993). The behaviour of sharks. *Reviews in Fish Biology and Fisheries, 3*, 133-159.

Brown, R. S., Cooke, S. J., Anderson, W. G., & McKinley, R. S. (1999). Evidence to challenge the "2% rule" for biotelemetry. *North American Journal of Fisheries Management, 19*, 867-871.

Butler, P. J., Green, J. A., Boyd, I. L., & Speakman, J. R. (2004). Measuring metabolic rate in the field: The pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology, 18*, 168-183.

Caine, N. G. (1990). Unrecognized anti-predator behaviour can bias observational data. *Animal Behaviour, 39*, 195-196.

Camhi, M. D., Valenti, S. V., Fordham, S. V., Fowler, S. L., & Gibson, C. (2009). *The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop*. IUCN Species Survival Commission's Shark Specialist Group. Newbury, UK, 78pp

Clark, T., Sandblom, E., Hinch, S., Patterson, D., Frappell, P., & Farrell, A. (2010). Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (*Oncorhynchus nerka*). *Journal of Comparative Physiology B, 180*, 673-684.

Compagno, L. J. V. (1984). FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. *FAO Fisheries Synopsis, 125,* 251-655.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., Butler, P. J. (2004). Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology & Evolution, 19*, 334-343.

Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: Relevance to regional, national, and IUCN red list threat assessments. *Endangered Species Research, 4*, 165-185.

Costa, D. P. (1993). The secret life of marine mammals. *Oceanography, 6*, 120-128.

Costa, D. P., & Sinervo, B. (2004). Field physiology: Physiological insights from animals in nature. *Annual Review of Physiology, 66*, 209-242.

Costa, D. P., Block, B. A., Bograd, S. J., Fedak, M. A., & Gunn, J. S. (2010). TOPP as a marine life observatory: Using electronic tags to monitor the movements, behaviour and habitats of marine vertebrates. *Procedings of OceanObs'09: Sustained Ocean Observations and Information for Society (Vol. 2),* Venice, Italy, 190-198.

Crew, H. (1908). *The Principles of Mechanics*. Longmans, Green and Co., New York, 295pp.

Cubero-Pardo, P., Herrón, P., & González-Pérez, F. (2011). Shark reactions to scuba divers in two marine protected areas of the eastern tropical Pacific. *Aquatic Conservation: Marine and Freshwater Ecosystems, 21*, 239-246.

da Silva, C. (2007). *The status and prognosis of the smoothhound shark (Mustelus mustelus) fishery in the southeastern and southwestern Cape coasts, South Africa.* Unpublished MSc, Rhodes University, South Africa, 162pp.

da Silva, C., & Bürgener, M. (2007). South Africa's demersal shark meat harvest. *TRAFFIC Bulletin, 21*, 55-66.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S., Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science, 283*, 993-996.

DuBois, A. B., Cavagna, G. A., & Fox, R. S. (1976). Locomotion of bluefish. *Journal of Experimental Zoology, 195*, 223-235.

DuBois, A. B., & Ogilvy, C. S. (1978). Forces on the tail surface of swimming fish: Thrust, drag and acceleration in bluefish (*Pomatomus saltatrix*). *Journal of Experimental Biology, 77*, 225-241.

Duntley, S. Q. (1952). *The Visibility of Submerged Objects*. Massachusetts Institute of Technology, Final Report. Visibility Laboratory, 74 pp.

Einstein, A. (1920). *Relativity: The Special and General Theory*. Henry Holt and Co., New York, 168 pp.

Elliot, K. H., Le Vaillant, M., Kato, A., Speakman, J. R., & Ropert-Coudert, Y. (2013). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology Letters, 9*, doi: 10.1098/rsbl.2012.0919.

Essapian, F. S. (1962). Notes on the behavior of sharks in captivity. *Copeia, 1962*, 457-459.

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods, 39*, 175-191.

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters, 13*, 1055-1071.

Ford, E. (1921). A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. *Journal of the Marine Biological Association of the United Kingdom, 12*, 468-505.

Freadman, M. A. (1981). Swimming energetics of striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*): Hydrodynamic correlates of locomotion and gill ventilation. *Journal of Experimental Biology, 90*, 253-265.

Gao, L., Campbell, H. A., Bidder, O. R., & Hunter, J. (2013). A web-based semantic tagging and activity recognition system for species' accelerometry data. *Ecological Informatics, 13*, 47-56.

Gleiss, A. C., Gruber, S. H., & Wilson, R. P. (2009). Multi-channel data-logging: Towards determination of behaviour and metabolic rate in free-swimming sharks. In J. L. Nielsen, N. Fragoso, M. Lutcavage, H. Arrizabalaga, A. Hobday & J. Sibert (Eds.), *Tagging and Tracking of Marine Animals with Electronic Devices,* Springer, Netherlands, 211-228.

Gleiss, A. C., Norman, B., Liebsch, N., Francis, C., & Wilson, R. P. (2009). A new prospect for tagging large free-swimming sharks with motion-sensitive data-loggers. *Fisheries Research, 97*, 11-16.

Gleiss, A. C., Dale, J. J., Holland, K. N., & Wilson, R. P. (2010). Accelerating estimates of activity-specific metabolic rate in fishes: Testing the applicability of acceleration data-loggers. *Journal of Experimental Marine Biology and Ecology, 385*, 85-91.

Gleiss, A. C., Norman, B., & Wilson, R. P. (2011). Moved by that sinking feeling: Variable diving geometry underlies movement strategies in whale sharks. *Functional Ecology, 25*, 595-607.

Gleiss, A. C., Wilson, R. P., & Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution, 2*, 23-33.

Gleiss, A. C., Jorgensen, S. J., Liebsch, N., Sala, J. E., Norman, B., Hays, G. C., Quintana, F., Grundy, E., Campagna, C., Trites, A. W., Block, B. A., Wilson, R. P. (2011). Convergent evolution in locomotory patterns of flying and swimming animals. *Nature Communications, 2*, 352.

Gómez Laich, A., Wilson, R. P., Quintana, F., & Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research, 10*, 29-37.

Goodall, J. (1968). *The Behaviour of Free-living Chimpanzees in the Gombe Stream Reserve*. Baillière, Tindall & Cassell, London, 161-311.

Goosen, A. J. J., & Smale, M. J. (1997). A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). *South African Journal of Marine Science, 18*, 85-91.

Graps, A. (1995). An introduction to wavelets. *IEEE Computational Science & Engineering, 2*, 50-61.

Green, J. A., Halsey, L. G., Wilson, R. P., & Frappell, P. B. (2009). Estimating energy expenditure of animals using the accelerometry technique: Activity, inactivity and comparison with the heart-rate technique. *Journal of Experimental Biology, 212*, 471-482.

Gruber, S. H., & Myrberg, A. A. (1977). Approaches to the study of the behavior of sharks. *American Zoologist, 17*, 471-486.

Grünewälder, S., Broekhuis, F., Macdonald, D. W., Wilson, A. M., McNutt, J. W., Shawe-Taylor, J., Hailes, S. (2012). Movement activity based classification of animal behaviour with an application to data from cheetah *(Acinonyx jubatus)*. *PLoS ONE, 7*, e49120.

Halsey, L. G., Shepard, E. L. C., Hulston, C. J., Venables, M. C., White, C. R., Jeukendrup, A. E., Wilson, R. P. (2008). Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: Tests with an easy model species, *Homo sapiens*. *Zoology, 111*, 231-241.

Halsey, L. G., Shepard, E. L. C., Quintana, F., Gomez Laich, A., Green, J. A., & Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology Part A, 152*, 197-202.

Hammerschlag, N., Gallagher, A. J., & Lazarre, D. M. (2011). A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology, 398*, 1-8.

Hammerschlag, N., & Sulikowski, J. (2011). Killing for conservation: The need for alternatives to lethal sampling of apex predatory sharks. *Endangered Species Research, 14*, 135-140.

Heithaus, M. R., Marshall, G. J., Buhleier, B. M., & Dill, L. M. (2001). Employing crittercam to study habitat use and behavior of large sharks. *Marine Ecology Progress Series, 209*, 307-310.

Henningsen, A. D. (1994). Tonic immobility in 12 elasmobranchs: Use as an aid in captive husbandry. *Zoo Biology, 13*, 325-332.

Hobson, E. S. (1963). Feeding behavior in three species of sharks. *Pacific Science, 17*, 171-194.

Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R., & Fournier, D. A. (1992). Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature, 358*, 410-412.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 19060-19065.

Hooker, S. K., & Boyd, I. L. (2003). Salinity sensors on seals: Use of marine predators to carry CTD data loggers. *Deep Sea Research Part I: Oceanographic Research Papers, 50*, 927-939.

Jain, A. K., Murty, M. N., & Flynn, P. J. (1999). Data clustering: A review. *ACM Computing Surveys, 31*, 264-323.

Jewell, O. J. D., Wcisel, M. A., Gennari, E., Towner, A. V., Bester, M. N., Johnson, R. L., Singh, S. (2011). Effects of smart position only (SPOT) tag deployment on white sharks *Carcharodon carcharias* in South Africa. *PLoS ONE, 6*, e27242.

Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering, 28*, 3-12.

Johnson, R. H., & Nelson, D. R. (1973). Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. *Copeia, 1973*, 76-84.

Kawabe, R., Nashimoto, K., Hiraishi, T., Naito, Y., & Sato, K. (2003a). A new device for monitoring the activity of freely swimming flatfish, Japanese flounder *Paralichthys olivaceus*. *Fisheries Science, 69*, 3-10.

Kawabe, R., Kawano, T., Nakano, N., Yamashita, N., Hiraishi, T., & Naito, Y. (2003b). Simultaneous measurement of swimming speed and tail beat activity of

free-swimming rainbow trout *Oncorhynchus mykiss* using an acceleration data-logger. *Fisheries Science, 69*, 959-965.

Kawabe, R., Naito, Y., Sato, K., Miyashita, K., & Yamashita, N. (2004). Direct measurement of the swimming speed, tailbeat, and body angle of Japanese flounder (*Paralichthys olivaceus*). *ICES Journal of Marine Science, 61*, 1080-1087.

Kawatsu, S., Sato, K., Watanabe, Y., Hyodo, S., Breves, J. P., Fox, B. K., Grau, E. G., Miyazaki, N. (2010). A new method to calibrate attachment angles of data loggers in swimming sharks. *EURASIP Journal on Advances in Signal Processing,* doi:10.1155/2010.

King, A. M., Loiselle, D. S., & Kohl, P. (2004). Force generation for locomotion of vertebrates: Skeletal muscle overview. *IEEE Journal of Oceanic Engineering, 29*, 684-691.

Koob, T. J. (2004). Elasmobranchs in the public aquarium: 1860 to 1930. In M. Smith, D. Warmolts, D. Thoney & R. Heuter (Eds.), *Elasmobranch Husbandry Manual: Captive Care of Sharks, Rays, and their Relatives,* Ohio Biological Survey, Inc., Columbus, Ohio, 1-14.

Kooyman, G. L. (1965). Techniques used in measuring diving capacities of Weddell seals. *Polar Record, 12*, 391-394.

Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., & Podesta, M. (2001). Collisions between ships and whales. *Marine Mammal Science, 17*, 35-75.

Laroche, R. K., Kock, A. A., Dill, L. M., & Oosthuizen, W. H. (2007). Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. *Marine Ecology Progress Series, 338*, 199-209.

Lingham-Soliar, T. (2005). Dorsal fin in the white shark, *Carcharodon carcharias*: A dynamic stabilizer for fast swimming. *Journal of Morphology, 263*, 1-11.

Lowry, M., Folpp, H., Gregson, M., Suthers, I. (2012). Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. *Journal of Experimental Marine Biology and Ecology, 416,* 243-253.

Magnan, P. (1991). Unrecognized behavior and sampling limitations can bias field data. *Environmental Biology of Fishes, 31,* 403-406.

Mannini, A., & Sabatini, A. M. (2010). Machine learning methods for classifying human physical activity from on-body accelerometers. *Sensors, 10*, 1154-1175.

Marshall, H., Field, L., Afiadata, A., Sepulveda, C., Skomal, G., & Bernal, D. (2012). Hematological indicators of stress in longline-captured sharks. *Comparative Biochemistry and Physiology Part A, 162*, 121-129.

Martin, R. A., Hammerschlag, N., Collier, R. S., & Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at seal island, South Africa. *Journal of the Marine Biological Association of the United Kingdom, 85*, 1121-1134.

Martin, R. A. (2007). A review of shark agonistic displays: Comparison of display features and implications for shark-human interactions. *Marine and Freshwater Behaviour and Physiology, 40*, 3-34.

McLaughlin, R. H., & O'Gower, A. K. (1971). Life history and underwater studies of a heterodont shark. *Ecological Monographs, 41*, 271-289.

Meijer, G. A., Westerterp, K. R., Koper, H., & ten Hoor, F. (1989). Assessment of energy expenditure by recording heart rate and body acceleration. *Medicine and Science in Sports and Exercise, 21*, 343-347.

Meyer, C. G., Clark, T. B., Papastamatiou, Y. P., Whitney, N. M., & Holland, K. N. (2009) Long-term movement patterns of tiger sharks *Galeocerdo cuvier* in Hawaii. *Marine Ecology Progress Series, 381*, 223-235.

Murchie, K. J., Cooke, S. J., Danylchuk, A. J., Suski, C. D. (2011). Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. *Journal of Experimental Marine Biology and Ecology*, *396,* 147-155.

Murru, F. L. (1990). The care and maintenance of elasmobranchs in controlled environments. In H. L. Pratt Jr., S. H. Gruber & T. Taniuchi (Eds.), *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* NOAA Technical Report NMFS 90, 203-209.

Naesje, T. F., Cowley, P. D., Diserud, O. H., Childs, A.-R., Kerwath, S. E., Thorstad, E. B. (2012). Riding the tide: estuarine movements of a sciaenid fish, *Argyrosomus japonicus*. *Marine Ecology Progress Series, 460*, 221-232.

Naito, Y. (2004). New steps in bio-logging science. *Memoirs of the National Insititue of Polar Research, Special Issue, 58*, 50-57.

Naito, Y., Bornemann, H., Takahashi, A., McIntyre, T., & Plötz, J. (2010). Fine-scale feeding behavior of Weddell seals revealed by a mandible accelerometer. *Polar Science, 4*, 309-316.

Nakamura, I., Watanabe, Y. Y., Papastamatiou, Y. P., Sato, K., & Meyer, C. G. (2011). Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*. *Marine Ecology Progress Series, 424*, 237-246.

Nakaya, K. (1995). Hydrodynamic function of the head in the hammerhead sharks (Elasmobranchii: Sphyrnidae). *Copeia, 1995*, 330-336.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 19052-19059.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M., & Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: General concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology, 215*, 986-996.

Nelson, D. R. (1977). On the field study of shark behavior. *American Zoologist, 17*, 501-507.

Nelson, D. R. (1978). Telemetering techniques for the study of free-ranging sharks. In E. S. Hodgson, & R. F. Mathewson (Eds.), *Sensory Biology of Sharks, Skates, and Rays*. Office of Naval Research, Arlington, VA, 419-482.

Noldus, L. P. J. J., Trienes, R. J. H., Hendriksen, A. H. M., Jansen, H., & Jansen, R. G. (2000). The observer video-pro: New software for the collection, management, and presentation of time-structured data from videotapes and digital media files. *Behavior Research Methods, Instruments, & Computers, 32*, 197-206.

Norton, F. H., & Warner, E. P. (1921). *Accelerometer design.* Report No. 100. Langley Memorial Aeronautical Laboratory, Langley Field, VA, 489-504.

Nowacek, D. P., Johnson, M. P., Tyack, P. L., Shorter, K. A., McLellan, W. A., & Pabst, D. A. (2001). Buoyant balaenids: The ups and downs of buoyancy in right whales. *Proceedings of the Royal Society B, 268*, 1811-1816.

O'Dor, R., Dagorn, L., Holland, K., Jonsen, I. D., Payne, J., Sauer, W., Semmens, J., Stokesbury, M., Smith, P., Whoriskey, F. (2010). The ocean tracking network. *Procedings of OceanObs'09: Sustained Ocean Observations and Information for Society (Vol. 2),* Venice, Italy, 724-732.

Okuyama, J., Kawabata, Y., Naito, Y., Arai, N., & Kobayashi, M. (2009). Monitoring beak movements with an acceleration datalogger: A useful technique for assessing the feeding and breathing behaviors of sea turtles. *Endangered Species Research, 10*, 39-45.

Ollason, J. C., & Dunnet, G. M. (1980). Nest failures in the fulmar: The effect of observers. *Journal of Field Ornithology, 51*, 39-54.

Payne, N. L., Gillanders, B. M., Seymour, R. S., Webber, D. M., Snelling, E. P., Semmens, J. M. (2011). Accelerometry estimates field metabolic rate in giant Australian cuttlefish *Sepia apama* during breeding. *Journal of Animal Ecology, 80,* 422-420.

Postlethwaite, C. M., Dennis, T. E. (2103). Effects of temporal resolution on an inferential model of animal movement. *PLoS ONE, 8,* e57640.

R Development Core Team. (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, R. A., & Rasmussen, L. E. (1967). Some observations on the protein and enzyme levels and fractions in normal and stressed elasmobranchs. *Transactions of the New York Academy of Sciences, 29*, 397-413.

Ritter, E. K., & Brunnschweiler, J. M. (2003). Do sharksuckers, echeneis naucrates, induce jump behaviour in blacktip sharks, *Carcharhinus limbatus*? *Marine and Freshwater Behaviour and Physiology, 36*, 111-113.

Roberts, J. L. (1975). Active branchial and ram gill ventilation in fishes. *Biology Bulletin, 148, 85-105.*

Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P. G., Naito, Y., & Le Maho, Y. (2004). A fine-scale time budget of cape gannets provides insights into the foraging strategies of coastal seabirds. *Animal Behaviour, 67*, 985-992.

Ropert-Coudert, Y., & Wilson, R. P. (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment, 3*, 437-444.

Ropert-Coudert, Y., Knott, N., Chiaradia, A., & Kato, A. (2007). How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep-Sea Research Part II: Topical Studies in Oceanography, 54*, 415-423.

Rosenthal, R. (1966). *Experimenter Effects in Behavioral Research.* Appleton-Century-Crofts, New York, 464 pp.

Roylance, L. M., & Angell, J. B. (1979). A batch-fabricated silicon accelerometer. *IEEE Transactions on Electron Devices, 26*, 1911-1917.

Rutz, C., & Hays, G. C. (2009). New frontiers in biologging science. *Biology Letters, 5*, 289-292.

Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., Wanless, S. (2009). Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE, 4*, e5379.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B., & Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology, 206*, 1461-1470.

Sato, K., Charrassin, J.-B., Bost, C.-A., & Naito, Y. (2004). Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *Journal of Experimental Biology, 207*, 4057-4065.

Scholander, P. F. (1940). *Experimental Investigations on the Respiratory Function in Diving Mammals and Birds*. Hvalradets Skrifter, Oslo, Norway, 131 pp.

Schwarz, G. (1978). Estimating the dimension of a model. *Annals of Statistics, 6,* 461-464.

Serena, F., Mancusi, C., Clò, S., Ellis, J. & Valenti, S. V. (2004). *Mustelus mustelus.* Accessed 13 October 2011, from www.iucnredlist.org

Shepard, E. L. C., Wilson, R. P., Halsey, L. G., Quintana, F., Laich, A. G., Gleiss, A. C., Liebsch, N., Myers, A. E., Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology, 4*, 235-241.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A. C., Morgan, D. T., Myers, A. E., Newman, C., Macdonald, D. W. (2010). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research, 10*, 47–60.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. Z., Brierley, A. S., Hindell, M. A., Morritt, D., Musyl, M. K., Righton, D., Shepard, E. L. C., Wearmouth, V. J., Wilson, R. P., Witt, M. J., Metcalfe, J. D. (2008). Scaling laws of marine predator search behaviour. *Nature, 451*, 1098-1102.

Sims, D. W. (2012). Tracking and analysis techniques for understanding free-ranging shark movements and behaviour. In J. C. Carrier, J. A. Musick & M. R. Heithaus (Eds.), *Biology of Sharks and their Relatives* (2nd ed.). CRC Press. Boca Raton, FL, 351-392.

Skomal, G. B., & Chase, B. C. (2002). The physiological effects of angling on post-release survivorship in tunas, sharks, and marlin [Abstract]. *American Fisheries Society Symposium, 30* 135-138.

Smale, M. J. (1997). Trade in sharks and shark products in South Africa. In N. T. Marshall, & R. Barnett (Eds.), *Trade in Shark and Shark Products in the Western Indian and Southeast Atlantic Oceans.* TRAFFIC East/Southern Africa, Nairobi, Kenya, 80-100.

Smale, M. J., & Compagno, L. J. V. (1997). Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* (Smith, 1957) (pisces: Triakidae). *South African Journal of Marine Science, 18*, 229-248.

Smale, M. J., Jones, R. T., Correia, J. P., Henningsen, A. D., Crow, G. L., & Garner, R. (2004). Research on elasmobranchs in public aquariums. In M. Smith, D. Warmolts, D. Thoney & R. Heuter (Eds.), *Elasmobranch Husbandry Manual: Captive Care of Sharks, Rays, and their Relatives*. Ohio Biological Survey, Inc., Columbus, OH, 533-541.

Standora Jr., E. A., Sciarrotta, T. C., Ferrel, D. W., Carter, H. C., & Nelson, D. R. (1972). *Development of a multichannel, ultrasonic telemetry system for the study of shark behavior at sea.* Technical Report No. 5. California State University, Long Beach Foundation, Long Beach, CA, 69pp.

Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science, 57*, 476-494.

Stoner, A. W., Ryer, C. H., Parker, S. J., Auster, P. J., Wakefield, W. W. (2008). Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Canadian Journal of Fisheries and Aquatic Sciences, 65,* 1230-1243.

Strasburg, D. W. (1958). Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. *Fisheries, 58*, 335-361.

Strong, W. R., Murphy, R. C., Bruce, B. D., & Nelson, D. R. (1992). Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: A preliminary report. *Marine and Freshwater Research, 43*, 13-20.

Tanaka, H., Takagi, Y., & Naito, Y. (2001). Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *Journal of Experimental Biology, 204*, 3895-3904.

Thiebault, A., Tremblay, Y. (2013). Splitting animal trajectories into fine-scale behaviorally consistent movement units: breaking points relate to external stimuli in a foraging seabird. *Behavioral Ecology and Sociobiology, 67*, 1013-1026.

Thompson, A. A., & Mapstone, B. D. (1997). Observer effects and training in underwater visual surveys of reef fishes. *Marine Ecology Progress Series, 154*, 53-63.

Trefethen, P. S., & Dudley, J. W. (1957). Ultrasonic tracer follows tagged fish. *Electronics, 30*, 156-160.

Tsuda, Y., Kawabe, R., Tanaka, H., Mitsunaga, Y., Hiraishi, T., Yamamoto, K., Nashimoto, K. (2006). Monitoring the spawning behaviour of chum salmon with an acceleration data logger. *Ecology of Freshwater Fish, 15*, 264-274.

Uchida, S., Toda, M., & Kamel, Y. (1990). Reproduction of elasmobranchs in captivity. In H. L. Pratt Jr., S. H. Gruber & T. Taniuchi (Eds.), *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* NOAA Technical Report NMFS 90, 211-237.

Watanabe, S., Izawa, M., Kato, A., Ropert-Coudert, Y., & Naito, Y. (2005). A new technique for monitoring the detailed behaviour of terrestrial animals: A case study with the domestic cat. *Applied Animal Behaviour Science, 94*, 117-131.

Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y., & Miyazaki, N. (2006). Body density affects stroke patterns in Baikal seals. *Journal of Experimental Biology, 209*, 3269-3280.

Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K., & Naito, Y. (2003). Stroke and glide of wing-propelled divers: Deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proceedings of the Royal Society B, 270*, 483-488.

Weihs, D. (1973). Mechanically efficient swimming techniques for fish with negative buoyancy. *Journal of Marine Research, 31*, 194-209.

Weihs, D. (1974). Energetic advantages of burst swimming of fish. *Journal of Theoretical Biology, 48*, 215-229.

Whitney, N. M., Papastamatiou, Y. P., Holland, K. N., & Lowe, C. G. (2007). Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus*. *Aquatic Living Resources, 20*, 299-305.

Whitney, N. M., Pratt Jr, H. L., Pratt, T. C., & Carrier, J. C. (2010). Identifying shark mating behaviour using three-dimensional acceleration loggers. *Endangered Species Research, 10*, 71-82.

Whitney, N. M., Papastamatiou, Y. P., & Gleiss, A. C. (2012). Integrative multisensor tagging: Emerging techniques to link elasmobranch behaviour, physiology, and ecology. In J. C. Carrier, J. A. Musick & M. R. Heithaus (Eds.), *Biology of Sharks and their Relatives* (2nd ed.). CRC Press, Boca Raton, FL, 265-290.

Williams, T. M., Fuiman, L. A., Horning, M., & Davis, R. W. (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: Pricing by the stroke. *Journal of Experimental Biology, 207*, 973-982.

Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J., Croll, D. A. (2000). Sink or swim: Strategies for cost-efficient diving by marine mammals. *Science, 288*, 133-136.

Wilson, R. P., Grant, W. S., & Duffy, D. C. (1986). Recording devices on free-ranging marine animals: Does measurement affect foraging performance? *Ecology, 67*, 1091-1093.

Wilson, R. P., Grémillet, D., Syder, J., Kierspel, M. A. M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J. A., Bost, C.-A., Plötz, J., & Nel, D. (2002). Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series, 228*, 241-261.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology, 75*, 1081-1090.

Wilson, R. P., Shepard, E. L. C., & Liebsch, N. (2008). Prying into the intimate details of animal lives: Use of a daily diary on animals. *Endangered Species Research, 4*, 123-137.

Winter, J. D. (1983). Underwater biotelemetry. In L. A. Nielsen, & D. L. Johnson (Eds.), *Fisheries Techniques*. American Fisheries Society, Bethesda, MD, 371-395.

Wolcott, T. G. (1995). New options in physiological and behavioural ecology through multichannel telemetry. *Journal of Experimental Marine Biology and Ecology, 193*, 257-275.

Wold, H. (1956). Causal inference from observational data: A review of end and means. *Journal of the Royal Statistical Society A, 119*, 28-61.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C., Le Maho, Y., Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology, 202*, 3121-3126.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M., Le Maho, Y. (2001). A new technique for monitoring the behaviour of free-ranging adelie penguins. *Journal of Experimental Biology, 204*, 685-690.

Young, F. A., Kajiura, S. M., Visser, G. J., Correia, J. P. S., & Smith, M. F. L. (2002). Notes on the long-term transport of the scalloped hammerhead shark (*Sphyrna lewini*). *Zoo Biology, 21*, 243-251.